UNIVERSITÉ DU QUÉBEC À RIMOUSKI

ANALYSE EN ISOTOPES STABLES DE LA MACROFAUNE BENTHIQUE ET DE SES SOURCES DE NOURRITURE DANS LES ENVIRONNEMENTS LITTORAUX LACUSTRES BORÉAUX

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RÉSUMÉ

Les milieux littoraux sont une composante importante des écosystèmes lacustres. Si de nombreuses études récentes portent sur les réseaux trophiques pélagiques, très peu considèrent les réseaux trophiques benthiques en milieu littoral. Le milieu littoral est alimenté par du carbone autochtone et allochtone, et il n'existe pas de consensus quant à l'importance relative de ces sources de carbone dans l'alimentation des invertébrés benthiques. Par ailleurs, il n'y a pas non plus de consensus quant à l'importance des macrophytes dans le réseau trophique benthique littoral. Les objectifs de cette étude sont donc d'évaluer le régime alimentaire des macro-invertébrés benthiques littoraux, dans des milieux contenant des macrophytes et des milieux avec un substrat nu, et de déterminer la position trophique des macro-invertébrés présents dans le milieu littoral benthique. Pour répondre à ces objectifs, sept lacs ont été échantillonnés en juin-juillet 2009. Pour chaque lac, il y a eu trois sites contenant des macrophytes et trois sites avec un substrat nu. Pour déterminer les régimes alimentaires des différents organismes, des isotopes stables de carbone et azote ont été mesurés pour chaque source de nourriture potentielle ainsi que pour les macro-invertébrés et des analyses par modèle de mélange ont été effectuées. Les résultats obtenus montrent que les apports terrigènes sont très importants. En effet, que ce soit en présence ou non de macrophytes, la principale source de nourriture des invertébrés détritivores/herbivores est constituée par des détritus de feuilles de plantes terrestres. Lorsque les macrophytes sont présents, leur forme détritique apparaît comme deuxième source de nourriture. Les macrophytes vivants et le périphyton sont, quant à eux, des sources de nourriture moins importantes dans le régime alimentaire des invertébrés détritivores/herbivores. Les régimes alimentaires des invertébrés omnivores et des invertébrés carnivores sont quant à eux plus variés. Par ailleurs, les résultats de $\delta^{15}N$ ont montré qu'il y a trois niveaux trophiques chez les invertébrés benthiques des lacs que nous avons étudiés.

Mots clés : Macro-invertébrés, réseaux trophiques, isotopes stables, zone littorale, lacs boréaux, carbone allochtone, carbone autochtone, macrophytes

ABSTRACT

Littoral environments are an important component of lake ecosystems. While many recent studies on pelagic food webs, few of them consider its benthic counterpart. The littoral environment is fuelled by autochthonous and allochthonous carbon, and there is no consensus about the relative importance of these carbon sources in the diet of benthic invertebrates. Moreover, there is no consensus on the importance of macrophytes in the littoral benthic food web. The objective of this study was to assess the diet of benthic macroinvertebrates, in environments containing macrophytes and environments with a bare substrate and to determine the trophic position of macroinvertebrates present in benthic littoral environnement. To meet these objectives, seven lakes were sampled in June-July 2009. For each lake, there were three sites with macrophytes and three sites with a bare substrate. To assess the diets of different organisms, stable isotopes of carbon and nitrogen were measured for each potential food source and for macroinvertebrates and mixing model analyses were performed. Results showed that terrigenous inputs are very important. Indeed, whether in presence or absence of macrophytes, the main food source for scavengers and herbivores invertebrates was made up of leaf litter of terrestrial plants. When macrophytes were present, their detritial form appeared as the second food source. Living macrophytes and periphyton, were less important sources of food in the diet of scavengers and herbivores invertebrates. The diet of omnivores and carnivores invertebrates in turn were more variable. In addition, results showed that there $\delta^{15}N$ three trophic levels in benthic invertebrates of the lakes that we studied.

Keywords : Macroinvertebrates, food web, stables isotopes, littoral zone, allocthonous carbon, autochtonous carbon, macrophytes

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INTRODUCTION GÉNÉRALE

Interfaces avec les écosystèmes terrestres, les habitats benthiques littoraux sont une composante critique des écosystèmes lacustres et constituent l'un des milieux les plus productifs de la planète (Schindler et Scheuerell 2002; Strayer et Findlay 2010). Les macro-invertébrés rencontrés dans ces habitats occupent une position particulière dans les réseaux trophiques en ce sens qu'ils peuvent utiliser la matière organique (MO) s'y trouvant sous forme vivante (microhétérotrophes, microalgues, macrophytes) ou sous forme morte (détritus de nature et d'origines diverses, et à différents stades de dégradation) (James *et al.* 2000a; Vos *et al.* 2002), servir d'intermédiaire dans le transfert de la production primaire vers les niveaux trophiques supérieurs (Vander Zanden et Vadeboncoeur 2002; Vadeboncoeur *et al.* 2002) et peuvent être exploités directement par l'homme (e.g. crustacés; Covich *et al.* 2004). Malgré tout, le rôle écologique de la zone benthique littorale, notamment son importance sur la structure et le fonctionnement des réseaux trophiques lacustres et sur les échanges de MO entre le milieu terrestre et l'habitat pélagique sont encore bien peu connus à ce jour (Vadeboncoeur *et al.* 2002). Pour parvenir à une bonne compréhension des flux de matière et d'énergie à l'échelle de l'écosystème lacustre, il faut, entre autre, déterminer l'origine de la MO acquise par les différentes composantes invertébrées du réseau trophique benthique littoral (Jansson *et al.* 2007). Certaines études ont tenté d'évaluer l'importance relative des sources de carbone de différentes origines dans les réseaux trophiques lacustres (Jones *et al.* 1998; Grey *et al.* 2001). Grey *et al.* (2000) ont montré que, pour les crustacés zooplanctoniques, l'importance relative des sources allochtones de carbone organique diminue avec l'augmentation du niveau trophique des lacs et quant à eux, les résultats de Giorgio et France (1996) sugère que le zooplancton se nourrit préférablement sur du carbone d'origine algual.

Comparativement à leurs pendants pélagiques, la contribution des sources de carbones allochtone et autochtone aux réseaux trophiques benthiques ont été peu étudiés.

Origine et nature de la matière organique à la base des réseaux trophiques lacustres

Les écosystèmes aquatiques peuvent être alimentés par du carbone organique provenant de deux sources distinctes. Du carbone autochtone produit par le processus de photosynthèse par des organismes autotrophes (e.g., macrophytes, périphyton et phytoplancton) présents dans l'écosystème, et du carbone allochtone produit en dehors puis importé dans l'écosystème (Pace *et al.* 2004; Herwig *et al.* 2004; Solomon *et al.* 2008 ; Strayer et Findlay 2010).

Les macrophytes sont une composante importante des environnements littoraux lacustres (Kelly et Hawes 2005). Ils peuvent influencer les caractéristiques physico-chimiques telles que les concentrations en oxygène et carbone organique dissout (DOC), le pH, la température et l'intensité lumineuse dans la colonne d'eau et le déplacement des masses d'eau (Wetzel 2001). Ils sont par ailleurs un important producteur primaire qui favorise également la croissance d'algues à sa surface (e.g., épiphytes) (James *et al.* 2000b), représentent un habitat pour les invertébrés et les communautés de poissons, et une protection pour les proies contre les prédateurs (Wetzel 2001; Reynolds 2008; Kelly et Hawes 2005). Finalement, les macrophytes participent à la productivité totale des lacs. Ainsi, en milieu oligotrophe, la productivité et la biomasse des poissons sont corrélées avec celles des macrophytes (Vander Zanden et Vadeboncoeur 2002). Par contre, il n'existe pas de consensus quant au rôle des macrophytes sur la structure et le fonctionnement des réseaux trophiques aquatiques. Certaines études ont montré que si les macrophytes sont abondants, ils ne contribueraient à l'apport de carbone dans la chaîne alimentaire qu'à l'état vivant (Lodge 1991 ; Bunn et Boon 1993). Bunn et Boon (1993) ont ainsi observé que les gastéropodes et les trichoptères (*Trichoptera*) *Leptoceridae* sp. se nourrissent d'une

combinaison d'épiphytes et de macrophytes vivants. Lodge (1991) indique par ailleurs que la consommation des macrophytes par les brouteurs, est assez importante pour avoir un impact sur la biomasse et la production primaire de ceux-ci. Suite à des observations en milieu naturel et à des expériences en laboratoire, McGaha (1952) a dénombré plus de 50 espèces d'invertébrés aquatiques se nourrissant de différentes espèces de macrophytes vivants. Ces invertébrés sont pour la plupart des herbivores broyeurs (McGaha 1952). Merrit et Cummins (1996) mentionnent, quant à eux, que 9 % des insectes aquatiques consomment des macrophytes vivants. Par contre, l'intensité de l'herbivorie par les invertébrés dépendrait des espèces de macrophytes. Jacobsen et Sand-Jensen (1992) ont effectué des observations dans trois lacs et sept rivières ; toutes les macrophytes *Potamogeton* sp. portaient des traces de broutage et 76% des plants avaient des marques de défoliation exédent 1% de la plante, tandis que seulement 61% les macropytes non *Potamogeton* ont été broutées et seulement 25% des observations avaient une défoliation de plus de 1%. De plus, certaines sections des macrophytes seraient préférées à d'autres et leur consommation serait variable selon les saisons (Lodge 1991 ; Jacobsen et Sand-Jensen 1992, 1995) ; 90 % des défoliations par le processus d'herbivorie se feraient sur des feuilles agées, tandis que les feuilles jeunes ne seraient pratiquement pas affectées par le broutage. Par ailleurs, chez trois espèces de macrophytes sur quatre ayant été examinées par Jacobsen et Sand-Jensen (1992), la défoliation dûe aux herbivores était plus marquée en juin qu'aux autres mois testés (i.e., mai et août), ces différences de broutage entre les mois seraient dûe principalement à l'abondance de macrophytes durant le mois de juin et le manque d'alternative de source de nourriture durant cette période. Étant donné que les macrophytes contribuent grandement au pool détritique en milieu lacustre, d'autres études se sont intéressées au rôle alimentaire qu'elles pouvaient avoir sous cet état. Keough *et al.* (1996) et Herwig *et al.* (2004) ont montré que les réseaux trophiques aquatiques littoraux seraient plutôt alimentés par du carbone fixé par le phytoplancton et que lorsqu'utilisées, les macrophytes seraient plutôt sous forme de détritus. Dans une revue de littérature, Newman (1991) rapporte que les détritus de macrophytes seraient des sources de nourriture pour les gastéropodes, les crustacés et les insectes. Par ailleurs, les insectes seraient les principaux

consommateurs des plantes aquatiques et les diptères (*Diptera*), les coléoptères (*Coleoptera*), les lépidoptères (*Lepidoptera*), les homéoptères (*Homoptera*) et les tricoptères serait les insectes qui en consomme les plus (Newman 1991). La consommation des macrophytes à l'état détritique serait fonction des espèces des plantes, des espèces des consommateurs, ainsi que du stade de développement des différents consommateurs (Newman 1991).

Les microalgues, qui comprennent le phytoplancton et le périphyton sont une source importante de nourriture pour de nombreuses espèces d'invertébrés benthiques (Merrit et Cummins 1996 ; James *et al.* 2000a ; Hadwen et Bunn 2004, 2005 ; Jaschinski *et al.* 2011). Les travaux de Merrit et Cummins (1996) ont montré qu'onze pour cent des insectes aquatiques se nourriraient de microalgues (Merrit et Cummins 1996). Hadwen et Bunn (2004, 2005) et James *et al.* (2000a) ont également montré que malgré l'abondance de sources de carbone allochtone et de macrophytes, le périphyton est généralement la source de carbone la plus consommée par les macro-invertébrés et les poissons littoraux en milieu oligotrophe. Dans l'étude d'Hadwen et Bunn (2005), le périphyton représentait de 48 à 70 % de la diète des trichoptères et des hémiptères (*Hemiptera*) étudiés. Jaschinski *et al.* (2011) ont montré que l'amphipode *Gammarus pulex* utilise principalement du périphyton comme source de nourriture. En moyenne, 66 % de sa diète serait constituée par de l'épiphyton, 19% par du péryphyton se trouvant dans le sable et 15% par des détritus de feuilles terrestres. Molina *et al.* (2011) ont, quant à eux, montré que le périphyton serait la source de carbone la plus importante pour les invertébrés benthiques dans les régions comprenant de la végétation, tandis que dans les régions n'ayant pas de macrophyte, ce serait la matière particulaire en suspension qui serait la source de nourriture la plus importante. De plus, dans les lacs peu profonds où la productivité phytoplanctonique est faible, le périphyton serait la source de nourriture la plus importante pour des consommateurs tels que les gastéropodes, les amphipodes et le zooplancton (Hecky et Hesslein 1995 ; James *et al.* 2000b).

En dehors des sources de du carbone autochtone, les écosystèmes aquatiques peuvent également être alimentés par du carbone provenant de l'environnement terrestre (Strayer et Findlay 2010). En effet, les écosystèmes sont ouverts et connectés les uns aux autres par des flux biotiques et abiotiques qui influencent non seulement leur structure et leur composition mais également leur dynamique (Wetzel 2001). En fait, la zone littorale des lacs reçoit et retient une grande quantité de MO provenant de l'environnnement terrestre (Strayer et Findlay 2010). Cet apport de MO, que l'on appelle aussi subside allochtone, est un type de flux qui consiste en une ressource qui peut (1) provenir d'un premier écosystème, (2) être utilisée par un végétal ou un consommateur provenant d'un second écosystème, (3) permettre à l'utilisateur de la ressource d'accroître la productivité de sa population et (4) altérer potentiellement la dynamique de l'interaction utilisateur/ressource dans le second écosystème (Polis *et al.* 1997). Des travaux récents ont montré que les subsides tels que la MO provenant d'environnements terrestres pouvaient alimenter les réseaux trophiques des lacs oligotrophes et atteindre, voire même excéder, les niveaux de production primaire autochtone (Caraco et Cole 2004; Carpenter *et al.* 2005). En effet, bien que la production primaire benthique soit importante pour les consommateurs invertébrés et les poissons juvéniles, la MO allochtone est aussi une source de nourriture importante (Hecky et Hesslein 1995; France 1995, 1997; Herwig *et al.* 2004). Cole *et al.* (2006) ont ainsi montré que 60 à 85 % de la production des macro-invertébrés est supportée par le carbone organique particulaire d'origine terrestre. Les impacts des apports de subsides allochtones sur les réseaux trophiques lacustres dépendraient par ailleurs de leur forme (dissoute ou particulaire), de la voie d'entrée dans le réseau trophique et des types de consommateurs présents dans le système (Cole *et al.* 2006). Pace *et al.* (2004) ont ainsi montré que le DOC d'origine terrestre est incorporé dans la chaîne alimentaire lacustre *via* les bactéries pour ensuite se retrouver chez des invertébrés comme les daphnies (*Daphnia* sp.) et chez les poissons. Le carbone organique particulaire d'origine terrestre est quant à lui incorporé dans la chaîne alimentaire aquatique par le zooplancton qui le transfère aux consommateurs secondaires et tertiaires dans la chaîne alimentaire benthique et pélagique (Carpenter *et al.* 2005). De plus, certains poissons littoraux dépendent des détritus terrestres

pour obtenir une partie de l'énergie qui leur est nécessaire, ce qui complexifie grandement les réseaux trophiques littoraux (France 1995, 1997).

De nombreux travaux suggèrent que les hétérotrophes du réseau trophique pélagique sont principalement alimentés par des sources de carbone allochtone, sous forme détritique, notamment dans les lacs ayant des apports élevés en carbone organique dissout (Jones 1992; Jones *et al.* 1999; Grey *et al.* 2001; Karlsson *et al.* 2003). Dans une étude menée dans 24 lacs couvrant une large gamme d'états trophiques, Grey *et al.* (2000) ont montré que l'augmentation de l'état trophique conduit à une plus forte dépendance du zooplancton vis-à-vis de la production phytoplanctonique. Dans les lacs oligotrophes peu profonds, les zones littorales sont souvent plus productives que les zones pélagiques (Vadeboncoeur *et al.* 2002). Dans ce type de lac, la contribution des sources de carbone autochtone à la diète des consommateurs devrait donc, être plus élevée chez les hétérotrophes du réseau benthique que ceux du réseau pélagique. Cependant, les zones littorales sont également connues pour recevoir des apports importants de carbone allochtone de la végétation riveraine et abriter des assemblages d'invertébrés déchiqueteurs, ce qui suggère l'existence d'un réseau trophique fonctionnant *via* les apports détritiques allochtones. Des études ont montré que les chironomides (*Chironomidae*), les trichoptères et les éphéméroptères (*Ephemeropterae*) utilisent principalement des détritus pour leur alimentation (Grey *et al.* 2004a ; Karlson et Byström 2005 ; Hershey *et al.* 2006 ; Solomon *et al.* 2008). Par contre la proportion de détritus utilisée varie en fonction de la profondeur de la zone littorale étudiée (Solomon *et al.* 2008 ; Grey *et al.* 2004b). La consommation de carbone allochtone peut donc être importante, selon les espèces présentes et selon le milieu.

Solomon *et al.* (2011) ont, quant à eux, montré que dans des lacs oligotrophes le carbone terrestre, le carbone pélagique et le carbone benthique contribuent tous au réseau trophique des lacs avec une importance qui varie en fonction des organismes et des

propriétés des écosystèmes. Il demeure par conséquent difficile de prédire la contribution des sources de carbone allochtone et autochtone à la diète des consommateurs benthiques des zones littorales (Hadwen et Bunn 2004). De plus, peu de travaux ont été menés pour estimer l'importance relative des sources de carbone allochtone (détritus d'origine terrestre) et autochtone (microalgues et macrophytes) pour les consommateurs des zones littorales lacustres (James *et al.* 2000a, b; Hadwen et Bunn 2004). Aussi une bonne connaissance du régime alimentaire des consommateurs primaires dans les environnements benthiques littoraux pourrait permettre une meilleure compréhension des contributions indirectes du carbone terrestre, pélagique et benthique au régime alimentaire des consommateurs secondaires et tertiaires et par le fait même à une meilleure compréhension du fonctionnement des écosystèmes littoraux.

Outil isotopique pour l'étude de l'architecture des réseaux trophiques

L'analyse des contenus stomacaux de même que les mesures de taux d'ingestion par utilisation des isotopes radioactifs sont deux méthodes couramment utilisées pour caractériser les sources de nourriture utilisées par les organismes et donc pour identifier les transferts de la MO au sein des réseaux trophiques. L'une des limitations de ces méthodes tient à la relative incertitude de faire la part entre ce qui a été simplement ingéré et ce qui a été effectivement assimilé par l'animal. L'une des façons d'identifier le type de nourriture assimilée consiste à analyser la composition en isotopes naturels stables des différentes composantes étudiées (James *et al.* 2000a ; Schindler et Lubetkin 2004). Cette méthode est couramment mise en œuvre dans les travaux portant sur les réseaux trophiques en rivière (Finlay *et al.* 2002 ; Anderson et Cabana 2007), en lac (France 1995, 1997), en estuaire (Cloern *et al.* 2002) et dans les sols (Schmidt *et al.* 2004). En effet, les isotopes stables témoignent de l'assimilation intégrée sur une certaine période de temps, celle-ci correspondant au taux de renouvellement du tissu d'un organisme (Kling *et al.* 1992). Cette approche est basée sur l'existence d'une relation étroite entre les compositions isotopiques du consommateur et celles des sources qui composent sa diète (Eggers et Jones 2000). En

fait, le ratio d'isotopes stables du carbone d'un consommateur est un reflet du ratio isotopique (plus ou moins 1 ‰) de sa source de nourriture, donc de sa source d'énergie (DeNiro et Epstein 1978; Peterson et Fry 1987; Jardine *et al.* 2003). Le ratio isotopique de l'azote permet, quant à lui, de déterminer la position du consommateur dans le réseau trophique étant donné qu'il y a un enrichissement d'environ 3,4 ‰ par niveau trophique (Minagawa et Wada 1984). Les rapports d'isotopes stables (e.g. $\delta^{13}C$ et $\delta^{15}N$) fournissent ainsi des informations sur l'origine et la transformation de la matière (Eggers et Jones 2000).

La contribution des différents types de nourriture à la diète des différents groupes d'invertébrés peut être estimée à l'aide des modèles de mélange linéaires pondérés. Un modèle de mélange linéaire pondéré (*concentration-weighted linear mixing model*) prend en compte la proportion de chacune des sources de nourriture dans le régime alimentaire et considère aussi le rapport C/N de chaque source (Phillips et Koch 2002). Ce modèle permet de transformer les rapports en isotopes stables en composition de la diète, étant donné que la signature isotopique d'un consommateur est le reflet de la signature de ses sources alimentaires et la proportion de ces sources dans sa diète. C'est ainsi que cette technique permet, d'une part, d'évaluer les sources de MO dans les écosystèmes et, d'autre part, d'identifier la composition du régime alimentaire d'un consommateur donné.

Objectifs

La contribution des détritus terrestres, des macrophytes et du périphyton à la diète des invertébrés benthiques littoraux lacustres est peu connue. De plus, les transferts de la matière organique aux consommateurs secondaires et tertiaires sont également peu connus. Cette étude, réalisée suivant une approche faisant intervenir des traceurs d'origine de la matière organique que sont les rapports d'isotopes stables naturels du carbone ($^{13}C/^{12}C$) et de l'azote ($^{15}N/^{16}N$), visait donc à améliorer notre compréhension des transferts de matière

et d'énergie au sein des réseaux trophiques benthiques littoraux. Les objectifs spécifiques étaient donc : 1) de caractériser la signature isotopique de carbone et de l'azote des principales composantes macro-invertébrées et des sources potentielles de nourriture dans des lacs boréaux; 2) d'estimer l'importance relative du carbone allochtone et du carbone autochtone dans le régime alimentaire des organismes benthiques littoraux dans des habitats avec et sans macrophytes dans ces mêmes lacs; et 3) d'établir la position trophique des principales composantes macro-invertébrés de ces lacs.

CHAPITRE 1
ANALYSE EN ISOTOPES STABLES DE LA MACROFAUNE BENTHIQUE ET DE SES SOURCES DE NOURRITURE DANS LES ENVIRONNEMENTS LITTORAUX LACUSTRES BORÉAUX

1.1 RESUME EN FRANÇAIS DE L'ARTICLE

Les milieux littoraux sont une composante importante des écosystèmes lacustres. Si de nombreuses études récentes portent sur les réseaux trophiques pélagiques, très peu considèrent les réseaux trophiques benthiques en milieu littoral. Le milieu littoral est alimenté par du carbone autochtone et allochtone, et il n'existe pas de consensus quant à l'importance relative de ces sources de carbone dans l'alimentation des invertébrés benthiques. Par ailleurs, il n'y a pas non plus de consensus quant à l'importance des macrophytes dans le réseau trophique benthique littoral. Les objectifs de cette étude sont donc d'évaluer le régime alimentaire des macro-invertébrés benthiques littoraux, dans des milieux contenant des macrophytes et des milieux avec un substrat nu, et de déterminer la position trophique des macro-invertébrés présents dans le milieu littoral benthique. Pour répondre à ces objectifs, sept lacs ont été échantillonnés en juin-juillet 2009. Pour chaque lac, il y a eu trois sites contenant des macrophytes et trois sites avec un substrat nu. Pour déterminer les régimes alimentaires des différents organismes, des isotopes stables de carbone et azote ont été mesurés pour chaque source de nourriture potentielle ainsi que pour les macro-invertébrés et des analyses par modèle de mélange ont été effectuées. Les résultats obtenus montrent que les apports terrigènes sont très importants. En effet, que ce soit en présence ou non de macrophytes, la principale source de nourriture des invertébrés détritivores/herbivores est constituée par des détritus de feuilles de plantes terrestres. Lorsque les macrophytes sont présents, leur forme détritique apparaît comme deuxième source de nourriture. Les macrophytes vivants et le périphyton sont, quant à eux, des sources de nourriture moins importantes dans le régime alimentaire des invertébrés détritivores/herbivores. Les régimes alimentaires des invertébrés omnivores et des invertébrés carnivores sont quant à eux plus variés. De plus, les résultats de $\delta^{15}N$ ont montré qu'il y a trois niveaux trophiques chez les invertébrés benthiques des lacs que nous avons étudiés.

Mots clés : Macro-invertébré, réseaux trophiques, isotopes stables, zone littorale, lacs boréaux, carbone allochtone, carbone autochtone, macrophytes

L'article «*Benthic food web structure of boreal lakes assessed by stable isotope analyses*» sera soumis à une revue avec comité de lecture. Cet article a été cooridigé par moi-même et le professeur Christian Nozais. En tant que premier auteur, mon travail a consisté à faire les analyses en laboratoire, interpréter les résultats et rédiger l'article. Le second auteur, le professeur Christian Nozais, a fourni l'idée originale, a effectué le travail sur le terrain, a contribué au développement de la méthode, ainsi qu'à la révision de l'article. Une partie des résultats de cet article ont été présentés au congrès de l'American Society of Limnology and Oceanography à Puerto Rico en février 2011 et au Colloque du Centre d'études Nordiques à Québec en février 2011.

1.2 BENTHIC FOOD WEB STRUCTURE OF BOREAL LAKES ASSESSED BY STABLE ISOTOPE ANALYSIS

Abstract

Littoral environments are an important component of lake ecosystems. While many recent studies on pelagic food webs, few of them consider its benthic counterpart. The littoral environment is fuelled by autochthonous and allochthonous carbon, and there is no consensus about the relative importance of these carbon sources in the diet of benthic invertebrates. Moreover, there is no consensus on the importance of macrophytes in the littoral benthic food web. The objective of this study was to assess the diet of benthic macroinvertebrates, in environments containing macrophytes and environments with a bare substrate and to determine the trophic position of macroinvertebrates present in benthic littoral environnement. To meet these objectives, seven lakes were sampled in June-July 2009. For each lake, there were three sites with macrophytes and three sites with a bare substrate. To assess the diets of different organisms, stable isotopes of carbon and nitrogen were measured for each potential food source and for macroinvertebrates and mixing model analyses were performed. Results showed that terrigenous inputs are very important. Indeed, whether in presence or absence of macrophytes, the main food source for scavengers and herbivores invertebrates was made up of leaf litter of terrestrial plants. When macrophytes were present, their detritial form appeared as the second food source. Living macrophytes and periphyton, were less important sources of food in the diet of scavengers and herbivores invertebrates. The diet of omnivores and carnivores invertebrates in turn were more variable. In addition, results showed that there $\delta^{15}N$ three trophic levels in benthic invertebrates of the lakes that we studied.

Keywords: Macroinvertebrate, food web, stables isotopes, littoral zone, allochtonous carbon, autochtonous carbon, macrophytes

Introduction

Littoral benthic macroinvertebrates are an important heterotrophic component of lake ecosystems and constitute a link between primary producers and upper trophic levels in the food web (Giani and Laville 1995; Weatherhead and James 2001). For instance, there is both direct (50 %) and indirect (i.e., feeding on zoobenthos-supported fishes) (15 %) consumption of zoobenthos by certain fishes (Vander Zanden and Vadeboncoeur 2002). Even piscivorous specialists tend to consume a significant amount of benthic macroinvertebrates (Beaudoin et al. 2001; Schindler and Scheuerell 2002). Therefore, the importance of benthic macroinvertebrates for upper trophic levels highlights the need to further explore their functional role (i.e., resource partitioning and transfer of organic matter) in lakes.

Lake ecosystems can be sustained by two distinct sources of organic carbon. Autochthonous carbon produced via the process of photosynthesis by autotrophs (e.g. microalgae and macrophytes) within the lake and allochthonous carbon (e.g. detritus) produced outside and imported into the lake ecosystem (Pace et al. 2004; Herwig et al. 2004; Solomon et al. 2008; Strayer and Findlay 2010). Macrophytes are an important autotrophic component of lake littoral environments (Kelly and Hawes 2005). Indeed, in the littoral zone, macrophytes influence the physico-chemical characteristics, are important primary producers promoting algal growth onto their surface (James *et al.* 2000b) and constitute a habitat for benthic invertebrates and fish communities, and a protection against predators (Wetzel 2001; Reynolds 2008; Kelly and Hawes 2005). Finally, macrophytes can significantly contribute to the overall productivity of lakes. In oligotrophic lakes, total productivity and fish biomass are correlated with those of macrophytes (Vander Zanden and Vadeboncoeur 2002). Currently, however, there is no consensus about the role of macrophytes in aquatic food webs. Studies have shown that when macrophytes are abundant in the littoral zone, they contribute to the carbon input into the food chain only when they are alive (Lodge 1991; Bunn and Boon 1993). Bunn and Boon (1993) reported

that snails and caddisflies (*Trichoptera*) *Leptoceridae* sp. feed on a combination of epiphytes and macrophytes. Also, in a literature review, Lodge (1991) indicates that the consumption of macrophytes is important enough to have an impact on biomass and primary production thereof. By ways of laboratory experiments and observations in the natural environment, McGaha (1952) has been able to list over 50 species of aquatic invertebrates that could be able to feed on different species of living macrophytes. These invertebrates are mostly herbivorous shredders (McGaha 1952). Merrit and Cummins (1996) reported that 9 % of aquatic insects consume living macrophytes. On the other hand, the intensity of herbivory by invertebrates depends on macrophytes species. Jacobsen and Sand-Jensen (1992) have made observations in three lakes and seven rivers, all macrophytes Potamogeton sp. showed signs of grazing and 76% of plants had signs of defoliation distances exceeding 1% of the plant, while only 61% of the macropytes non Potamogeton were grazed and only 25% of the observations had a defoliation of more than 1%. In addition, some section of the plants would be preferred to others and consumption of macrophytes would be seasonally variable (Lodge 1991; Jacobsen and Sand-Jensen 1992, 1995). Indeed, Jacobsen and Sand-Jensen (1992) found that 90 % of defoliation occurs on older leaves, while young leaves are hardly affected by grazing. Also, in three species out of four having been examined by Jacobsen and Sand-Jensen (1992), defoliation due to herbivores was greater in June than during other months tested (i.e., May and August), these diffefences between months are grazing mainly due to the abundance of macrophytes during the month of June and the low availability of alternative food resources. In contrast, other studies have obtained results that question these findings. For instance, Keough *et al.* (1996) and Herwig *et al.* (2004) showed that littoral aquatic food webs are rather fueled by the carbon fixed by phytoplankton, and when used, macrophytes are rather in the form of detritus (Mann 1988, Keough *et al.* 1996; Herwig *et al.* 2004). Indeed, macrophytes contribute greatly to detritus in aquatic environments (Newman 1991).

Microalgae, including phytoplankton and periphyton, are much smaller than macrophytes, but sometimes have a total production comparable to that of macrophytes (Hart and Lovvorn 2000). Microalgae are an important food source for many benthic invertebrates (Merrit and Cummins 1996; James *et al.* 2000a; Hadwen and Bunn 2004, 2005; Jaschinski *et al.* 2011). Hadwen and Bunn (2004, 2005) and James *et al.* (2000a) showed that despite the abundance of allochtonous carbon sources and macrophytes, periphyton is generally the source of carbon mostly consumed by fish and invertebrates in the littoral zone of oligotrophic lakes. In their study, Hadwen and Bunn (2005) reported that periphyton accounted for 48 to 70 % of the diet of caddisflies and hemipterans (*Hemiptera*) studied. In addition, Jaschinski *et al.* (2011) have found that the amphipod *Gammarus pulex* uses mainly periphyton as a food source. On average, 66% of its diet is made up of epiphyton, 19% of sand microflora and 15% of terrestrial leaf litter. Meanwhile, Molina *et al.* (2011) have found that periphyton is the most important carbon source for bentic invertebrates in areas including vegetation. Moreover, in shallow lakes exhibiting low phytoplankton productivity, periphyton is the most important source of food for snails, amphipods and zooplankton (Hecky and Hesslein 1995, James *et al.* 2000b).

As previously mentioned, littoral zones are also known to receive large inputs of allochthonous carbon from riparian vegetation and to shelter assemblages of invertebrate shredders, suggesting the occurrence of a food web fuelled, but not only, by allochthonous matter. For instance, in oligotrophic lakes, Cole *et al.* (2006) showed that between 60 and 85 % of benthic macroinvertebrates used allochtonous organic carbon to meet their energy requirements. In addition, other studies have shown that chironomids (*Chironomidae*), mayflies (*Ephemeropterae*) and caddisflies use mainly allochtonous detritus in their diet (Grey *et al.* 2004a; Karlsoon and Byström 2005, Hershey *et al.* 2006; Solomon *et al.* 2008). However, the proportion of terrestrial leaf litter used as food source depends on the depth of the littoral zone studied. So allochthonous carbon consumption can be significant, depending on the species and littoral area. So far, however, very few studies have been

conducted to estimate the relative importance of allochthonous carbon sources (detritus of terrestrial origin) and autochthonous (microalgae and macrophytes) to the diet of littoral freshwater macroinvertebrates (James *et al.* 2000a, b; Hadwen and Bunn 2004).

Isotopic tool for the study of network architecture trophic

One way to identify the type of food assimilated is to analyze the composition of natural stable isotopes of the different components studied (James *et al.* 2000a; Schindler and Lubetkin 2004). This method has was used for the study of several environments, other: river (Finlay *et al.* 2002; Anderson and Cabana 2007), lakes (France 1995, 1997), estuaries (Cloern *et al.* 2002) and in soils (Schmidt *et al.* 2004). Indeed, stable isotopes reflect the assimilation integrated over a certain period time, the latter corresponding to the rate of tissue turnover an organism (Kling *et al.* 1992). This approach is based on the existence of a close relationship between the compositions isotope consumer and those sources that comprise its diet (Eggers and Jones 2000). In fact, the ratio of stable isotopes carbon of a consumer is a reflection of the isotopic ratio (more or less 1 ‰) of its food source, therefore its energy source (DeNiro and Epstein 1978; Peterson and Fry 1987; Jardine *et al.* 2003). The isotope ratio of nitrogen allows in turn, determine the position of consumers in food web as there is an enrichment of approximately 3.4 ‰ by trophic level (Minagawa and Wada 1984). Reports stable isotope (e.g. $\delta^{13}C$ and $\delta^{15}N$) thus provide information on the origin and transformation of matter (Eggers and Jones 2000).

The relative contribution of the different food sources to the diet of the different invertebrates groups can be estimated with concentration-weighted linear mixing models. A concentration-weighted linear mixing model considers the proportion of each food sources in the diet and also considers the ratio C/N of each source (Phillips and Koch 2002). This model can transform stable isotope ratios in composition of the diet. This is possible because the isotopic signature of a consumer reflect the isotopic signature of its diet and the

proportion of each food source in its diet. Thus, this technique allows firstly, to evaluate sources and fluxes in the POM ecosystems and, secondly, to identify the diet of a specific consumer.

This work aims at characterizing the benthic food webs of seven boreal lakes and examining the relative importance of autochthonous and allochthonous sources of organic carbon in these food webs. To do so, we measured naturally occurring carbon and nitrogen stable isotope ratios of major components of benthic macroinvertebrate communities and their potential diet sources at various sites within the seven lakes. Also, we established the trophic position of macroinvertebrates with their stable nitrogen isotope signature.

Methods

Study area

The study was conducted on the Boreal Shield in the Bas-Saint-Laurent region (Quebec, Canada) (Figure 1), in june 2009. Five of the seven lakes sampled (Noir, de l'Est, Macpès, des Baies, Petit Touradi) are surrounded by mixed vegetation stand, one lake (Grand Ferré) is surrounded by mixed vegetation with a dominance of conifers and one lake (Neigette) is surrounded by hardwood stand.

Field sampling

Samples were collected in all lakes at three littoral sites with macrophytes (sites M) and three littoral sites without macrophytes (sites B). Physico-chemical parameters (dissolved oxygen, water temperature, pH and conductivity) were measured using a YSI 556MPS probe at each site and the water transparency was estimated with a Secchi disk at the deepest part in each lake. Water samples (4L) were collected at each littoral site at

50 cm below the water surface with an Alpha bottle for the determination of chlorophyll *a*, DOC, total phosphorus (TP), dissolved inorganic phosphorus and nitrogen (DIP and DIN, respectively), and dissolved organic matter (DOM). Macrophytes, terrestrial detritus (e.g., leaf litter, woody debris) and periphyton were collected by hand while sediments organic matter (SOM) was collected with a hand-corer. Benthic macroinvertebrates were sampled using a Turtox D-net with a mesh size of 500 µm. Zooplankton samples were collected in the littoral zone using a Wisconsin net with mesh size of 333 µm. The cladoceran *Daphnia* sp. was used as baseline organism, in order to obtain information on the isotopic signature of phytoplankton (i.e. assuming that *Daphnia* sp. is strictly herbivorous) and gastropods was used as baseline organism for the benthic macroinvertebrates. All samples were placed in cooler boxes and transported to the laboratory for processing.

Sample preparation and analyses

Water samples were filtered (250 ml or more) onto Whatman GF/F filters for the determination of chl *a* concentration. Chl *a* was extracted for 24 h in 90 % acetone, at 5°C in the dark without grinding and its concentration was determined using the method of Welschmeyer *et al.* (1994). For the determination of DOC, water subsamples were filtered through precombusted (500°C, 5 h) Whatman GF/F filters. The filtrate was collected in glass vials with teflon-lined caps and acidified with 10 µL of 25 % v/v H_3PO_4. The determination of DOC levels was made with a TOC-5000A analyzer (Shimadzu, Kyoto, Japan), following the protocol of Whitehead *et al.* (2000). DOC reference standards available from the Hansell's Certified Reference Materials (CRM) program was used to test the method. Total phosphorus (TP) was measured with a TOC-5000A analyzer (Shimadzu, Kyoto, Japan), using the molybdenum blue method (Staiton *et al.* 1977) after autoclaving 50 ml samples with 0.5 g of potassium persulfate for 1 h at 120°C. DIP (phosphate) and DIN (nitrate and nitrite) were determined by using an AutoAnalyzer (AA3, Bran+Luebbe, German) after filtering water samples through a 0.22 µm Sartorius filter.

The measurement of stable isotope ratios (e.g. $\delta^{13}C$ and $\delta^{15}N$) was done on the epilithon, epixylon, POM, DOM, SOM, macrophytes, terrestrial leaf litter, zooplankton and benthic invertebrates. The latter were sorted in the laboratory and identified to family with the identification keys of Thorp and Covich (2001) and Merrit and Cummins (1996). Living macrophytes were cleaned from epiphytes and only leaves were used in stable isotope analyses. All but POM samples were lyophilized and powdered before being weighed and encapsulated in tin foil cups (Costech Analytical Technology). Filter samples for POM were lyophilized and encapsulated in pressed tin capsules (5 x 9 mm) (Costech Analytical Technology).

Analyses of stable isotopes ratios of C ($\delta^{13}C$) and N ($\delta^{15}N$) for macrophytes, terrestrial detritus, SOM, DOM, POM, epilithon, epixylon, benthic macroinvertebrates and zooplankton were carried out at the Institut des sciences de la mer (ISMER, Rimouski, Quebec, Canada) using a COSTECH ECS 4010 Elemental Analyser coupled with a DeltaPlus XP Isotope Ratio Mass Spectrometer (IRMS, Thermo Electron Co). System control as well as acquisition and treatment of the data were carried out using the Isodat 2 software. Stable isotope ratios were expressed in δ notation as parts per thousand (‰) according to the equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios.

Standards used for the measurement of ^{13}C and ^{15}N were anhydrous caffeine (Sigma Chemical Co., St-Louis, USA), Mueller Hinton Broth (Becton Dickinson, USA) and

Nannochloropsis, respectively. These homemade standards were calibrated using standards from the National Institute of Standards and Technology (NIST, USA). Replicate analyses of standards gave analytical errors (SD) of ± 0.30 ‰ for C and ± 0.18 ‰ for N.

The isotopic ratio of nitrogen determines the consumer's position in the food web given that there is an enrichment of approximately 3.4 ‰ by trophic level (Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). The trophic position of a consumer is defined as a value (noninteger) that represents energy weighted number of trophic transfers of energy that leads to this consumer (Vander Zanden and Rasmussen 1999). If we use the primary consumer as the basis of the food chain (gastropod sp.), the trophic position is calculated as follows:

$$\text{Trophic position}_{\text{consumer}} = (\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{primary consumer}}) / 3.4 + 2$$

where $\delta^{15}N_{\text{consumer}}$ is the $\delta^{15}N$ value of the consumer for which the trophic position is estimated, $\delta^{15}N_{\text{primary consumer}}$ is the $\delta^{15}N$ of the gastropod, 2 is the expected trophic position of the organism used to estimate baseline $\delta^{15}N$ and we assume an enrichment of 3.4 ‰ by trophic level (Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). The trophic position of each consummer was therefore considered.

Data analyses

The relative contribution of the different food sources to the diet of the different invertebrates groups was estimated with concentration-weighted linear mixing models. A concentration-weighted linear mixing model considers the proportion of each food sources in the diet and also considers the ratio C/N of each source (Phillips and Koch 2002). This

model can transform stable isotope ratios in composition of the diet. This is possible because the isotopic signature of a consumer reflect the isotopic signature of its diet and the proportion of each food source in its diet. Thus, this model enables to determine the relative contribution of each food source to the diet of the different invertebrates. This analysis was done using an open source R package (SIAR, Parnell *et al.* 2010).

Results

Physico-chemical characteristics of the seven studied lakes

Physico-chemical data for the seven lakes, outlined in Table 1, somehow covered narrow ranges. TP and chl *a* concentrations are typical of oligo-mesotrophic lakes in this region.

Potential food sources and consumer signatures

Mean $\delta^{13}C$ values of all invertebrates, leaf litter, living and dead macrophytes, periphyton, SOM, DOM, POM from all seven lakes ranged from -42.0 to -4.4 ‰ (Figures 2 to 8) suggesting that the biological components occurring in the littoral zone depend on energy sources exhibiting very different isotopic compositions. Similarly, mean $\delta^{15}N$ values of all invertebrates, leaf litter, living and dead macrophytes, periphyton, sediments, DOM, POM from all seven lakes ranged from -6.6 to 12.8 ‰ (Figures 2 to 8).

Leaf litter, living and dead macrophytes, periphyton, SOM, and POM were considered as potential basal resources and exhibited broad ranges in $\delta^{13}C$ values. DOM was excluded as a potential basal food source since it was highly ^{13}C-enriched compared to comsumers. Indeed, mean $\delta^{13}C$ values of DOM varied between -20.5 and -4.5 ‰ (annexe 1), at sites M and between -16.0 and -4.4 ‰ (annexe 2) at sites B. On the other hand, SOM

were highly ^{13}C-depleted among all basal resources. Mean $\delta^{13}C$ values of sediment varied between -50.2 and -32.2 ‰ (Figures 2 to 8) at sites M and between -39.2 and -32.7 ‰ (Figures 2 to 8) at sites B. $\delta^{13}C$ values of epilithon varied between -26.6 and -11.1 ‰ (Figures 2 to 8) at sites M and between -30.8 and -13.9 ‰ (Figures 2 to 8) at sites B $\delta^{13}C$ values of epixylon varied between -28.7 and -22.6 ‰ (Figures 2 to 8) at sites M and between -30.6 and -22.9 ‰ (Figures 2 to 8) at sites B. The $\delta^{13}C$ signatures of leaf litter varied between -32.1 and -27.9 ‰ (Figures 2 to 8) at sites M and between -31.0 and -28.5 ‰ (Figures 2 to 8) at sites B. POM exhibited $\delta^{13}C$ values varying between -32.8 and -29.1 ‰ (Figures 2 to 8) at sites M and between -33.6 and -29.1 ‰ (Figures 2 to 8) at sites B. Finaly, at sites M, $\delta^{13}C$ signatures of living macrophytes varied between -26.8 and -22.1 ‰ (Figures 2 to 8) and those of dead macrophytes varied between -29.6 and -22.2 ‰ (Figures 2 to 8). For the zooplankton the value of $\delta^{13}C$ varied between -37.3 and -30.5 ‰ (Figures 2 to 8).

The $\delta^{15}N$ value of DOM varied between 0.1 and 3.11 ‰ (annexe 1), at sites M and between -0.4 and 3.11 ‰ (annexe 2) at sites B. The $\delta^{15}N$ value of SOM varied between -0.1 and 3.2 ‰ (Figures 2 to 8) at sites M and between 2.3 and 4.2 ‰ (Figures 2 to 8) at sites B. The $\delta^{15}N$ value of epilithon varied between -0.5 and 3.6 ‰ (Figures 2 to 8) at sites M and between -1.3 and 3.7 ‰ (Figures 2 to 8) at sites B and the epixylon varied between -0.2 and 4.6 ‰ (Figures 2 to 8) at sites M and between -0.6 and 4.3 ‰ (Figures 2 to 8) at sites B. The $\delta^{15}N$ value of leaf litter varied between -3.8 and 2.0 ‰ (Figures 2 to 8) at sites M and between -0.5 and -2.3 ‰ (Figures 2 to 8) at sites B. For the POM the value of $\delta^{15}N$ varied between 0.9 and 4.1 ‰ (Figures 2 to 8) at sites M and between 0.2 and 5.4 ‰ (Figures 2 to 8) at sites B. Finaly, at sites M, the $\delta^{15}N$ value of living macrophytes varied between -1.4 and 4.8 ‰ (Figures 2 to 8) and the $\delta^{15}N$ value of dead macrophytes varied between -6.6 and 4.3 ‰ (Figures 2 to 8). The dead macrophytes have the more variable $\delta^{15}N$ values. For the zooplankton the value of $\delta^{15}N$ varied between 0.9 and 7.8 ‰ (Figures

2 to 8).

Overall, $\delta^{13}C$ signatures of primary consumers (amphipods *H. azteca*, mayflies *Caenidae* sp., *Heptageneiidae* sp, and *Ephemerellidae* sp.) are generally in the same range at sites M and B (between -36.6 and -26.5 ‰ at sites M and between -36.1 and -25.5 ‰ at sites B) (Figures 2 to 8). The $\delta^{13}C$ value of *H. azteca* varied between -32.7 and -26.9 ‰ (Figures 2 to 8) at sites M and between -32.8 and -25.6 ‰ (Figures 2 to 8) at sites B. The $\delta^{13}C$ value of mayflies *Caenidae* sp. varied between -35.5 and -29.4 ‰ (Figures 2 to 8) at sites M and between -31.8 and -29.0 ‰ (Figures 2 to 8) at sites B. For the mayflies *Heptageneiidae* sp. the $\delta^{13}C$ value varied between -31.7 and -29.9 ‰ (Figures 2 to 8) at sites M and between -33.3 and -27.3 ‰ (Figures 2 to 8) at sites B. The $\delta^{13}C$ value of mayflies *Ephemerellidae* sp. varied between -34.4 and -29.1 ‰ (Figures 2 to 8) at sites M and between -34.1 and -28.8 ‰ (Figures 2 to 8) at sites B. Finaly for *Ephemeridae* sp. mayflies, the $\delta^{13}C$ value varied between -33.8 and -26.9 ‰ (Figures 2 to 8) at sites M and between -32.9 and -26.7 ‰ (Figures 2 to 8) at sites B. Caddisflies *Leptoceridae* sp. have the more variable $\delta^{13}C$ values and the more enriched and the more depleted $\delta^{13}C$ values. The $\delta^{13}C$ value of caddisflies *Leptoceridae* sp. varied between -39.4 and -21.0 ‰ (Figures 2 to 8) at sites M and between -33.6 and -25.8 ‰ (Figures 2 to 8) at sites B. The $\delta^{13}C$ value of *Hydracarian* sp. varied between -32.6 and -28.3 ‰ (Figures 2 to 8) at sites M and between -34.5 and -27.1 ‰ (Figures 2 to 8) at sites B. The $\delta^{13}C$ value of midges *Chironomidae* sp. varied between -36.6 and -29.4 ‰ (Figures 2 to 8) at sites M and between -34.2 and -25.5 ‰ (Figures 2 to 8) at sites B. For the dragonflies *Anisoptera Libellulidae* sp. the $\delta^{13}C$ value varied between -32.6 and -26.5 ‰ (Figures 2 to 8) at sites M and between -36.1 and -26.1 ‰ (Figures 2 to 8) at sites B. Finaly, for the damselflies *Zygoptera Coenagrionidae* sp. the $\delta^{13}C$ value varied between -33.6 and -28.4 ‰ (Figures 2 to 8) at sites M and between -33.1 and -26.1 ‰ (Figures 2 to 8) at sites B.

The values of $\delta^{15}N$ consumers are very different according to consumers. The $\delta^{15}N$

value of *H. azteca* varied between 0.6 and 6.0 ‰ (Figures 2 to 8) at sites M and between 0.8 and 6.0 ‰ (Figures 2 to 8) at sites B. The $\delta^{15}N$ value of mayflies *Caenidae* sp. varied between 1.0 and 6.2 ‰ (Figures 2 to 8) at sites M and between 0.6 and 6.7 ‰ (Figures 2 to 8) at sites B. For the mayflies *Heptageneiidae* sp. the $\delta^{15}N$ value varied between 1.6 and 6.5 ‰ (Figures 2 to 8) at sites M and between 1.9 and 6.0 ‰ (Figures 2 to 8) at sites B. The $\delta^{15}N$ value of mayflies *Ephemerellidae* sp. varied between 0.5 and 6.2 ‰ (Figures 2 to 8) at sites M and between -1.35 and 5.6 ‰ (Figures 2 to 8) at sites B. Finaly for the *Ephemeridae* sp. mayflies, the $\delta^{15}N$ value varied between 1.0 and 5.6 ‰ (Figures 2 to 8) at sites M and between 1.1 and 6.1 ‰ (Figures 2 to 8) at sites B. The caddisflies *Leptoceridae* sp. have the more variable $\delta^{15}N$ values and are the most ^{15}N-enriched consumers. The $\delta^{15}N$ value of caddisflies *Leptoceridae* sp. varied between 3.0 and 12.8 ‰ (Figures 2 to 8) at sites M and between 3.7 and 11.4 ‰ (Figures 2 to 8) at sites B. The $\delta^{15}N$ value of *Hydracarian* sp. varied between 5.1 and 10.5 ‰ (Figures 2 to 8) at sites M and between 3.3 and 10.2 ‰ (Figures 2 to 8) at sites B. The $\delta^{15}N$ value of midges *Chironomidae* sp. varied between 4.0 and 7.1 ‰ (Figures 2 to 8) at sites M and between 2.9 and 7.0 ‰ (Figures 2 to 8) at sites B. For the dragonflies *Anisoptera Libellulidae* sp. the $\delta^{15}N$ value varied between 2.4 and 7.6 ‰ (Figures 2 to 8) for sites M and between 3.2 and 8.2 ‰ (Figures 2 to 8) for sites B. Finally, for the damselflies *Zygoptera Coenagrionidae* sp. the $\delta^{15}N$ value varied between 4.7 and 9.5 ‰ (Figures 2 to 8) at sites M and between 4.1 and 9.2 ‰ (Figures 2 to 8) at sites B.

Trophic position

The trophic position of consumers has been calculated in lakes and sites where gastropods did occur since they were used as the baseline. Primary, secondary and tertiary consumers are present in all lakes (Table 4). Mean trophic positions were 1.71, 2.27 and 3.42, for primary, secondary and tertiary consumers, respectively (Table 4). Amphipods (*Hyalella azteca*), mayflies *Caenidaes* sp. and mayflies *Heptageneiidae* sp. are

herbivorous / scavengers (Merrit and Cummins 1996, Thorp and Covich 2001). Although mayflies *Ephemerellidae* sp. can be omnivorous (Merrit and Cummins 1996), a value of 1.63 suggests that mayflies are herbivorous / scavengers. The mayflies *Ephemeridae* sp. can also be omnivorous (Merrit and Cummins 1996), but their trophic position values are rather low (2.04). Midges *Chironomidae* sp. are omnivorous or carnivorous (Merrit and Cummins 1996) which is consistent with the values found (2.23). Damselflies (*Zygoptera Coenagrionidae* sp.) and dragonflies (*Anisoptera Libellulidae* sp.) have trophic positions of 2.79 and 2.28, respectively, confirming their status as secondary consumers. Finally, although caddisflies *Leptoceridae* sp. are considered to be omnivorous and carnivorous (Merrit and Cummins 1996), estimated trophic position values (3.42) suggest that the studied species are tertiary consumers and therefore carnivorous.

Potential contribution of food sources for consumers

The POM, DOM and SOM have been removed from calculation of the linear mixing models because they do not inform us about the type of material that is eaten by organisms. Mixing models were performed to evaluate the carbon contribution to benthic primary consumers (amphipod *Hyalella azteca*, mayflies *Caenidae* sp., *Ephemerellidae* sp. and *Heptageneiidae* sp.) and showed that they seemed to derive their biomass carbon from terrestrial leaf litter with feasible contributions varying between 18 and 35 % at sites M (Table 2) and between 22 and 58 % at sites B (Table 3). Also, at sites M, the main contributors to the diet of primary consumers were dead macrophytes (up to 33 %) except for *H. azteca* and mayflies *Caenidae* sp. in lake Des Baies. In lake Des Baies at site M, *H. azteca* amphipods seem to derive their biomass carbon from leaf litter (26 %) while mayflies *Caenidae* sp. seem to derive their biomass carbon from living and dead macrophytes (20 and 19 % respectively), epilithon (20 %), epixylon (20 %) and leaf litter (20%) in equal proportion.

Mixing models were also performed to evaluate the carbon contribution to secondary and tertiary consumers (Tables 2 and 3). The common contributor to the diet of mayflies *Ephemeridae* sp. was terrestrial leaf litter (up to 54 %) (lakes de l'Est and Touradi for sites B and lakes Des Baies, Ferré and Touradi for sites M), but they also ate amphipods *H. azteca* (up to 25 %), mayflies *Caenidae* sp. (up to 33 %) and *Ephemerellidae* sp. (up to 34 %). For midges *Chironomidae* sp. the common contributor to the diet was terrestrial leaf litter (up to 46 %) (lakes Noir, Neigette, de l'Est and Touradi for sites B, and lakes Noir, Neigette and Ferré for sites M), they also ate amphipods *H. azteca* (up to 26 %), mayflies *Caenidae* sp. (up to 32 %), *Ephemerellidae* sp. (up to 35 %) and *Heptageneiidae* sp. (up to 28 %). For caddisflies *Leptoceridae* sp., dragonflies (*Anisoptera Libellulidae* sp.) and damselflies (*Zygoptera Coenagrionidae* sp.) there was no source more frequently than others. For caddisflies *Leptoceridae* sp. they ate mainly mayflies *Ephemerellidae* sp. (up to 37 %), *Caenidaes* sp. (up to 34 %), *Heptageneiidae* sp. (up to 37 %) and *Ephemeridae* sp. (up to 36 %), amphipods *H. azteca* (up to 36 %) and midges *Chironomidae* sp. (up to 31 %). For dragonflies *Anisoptera Libellulidae* sp. they ate mainly amphipods *H. azteca* (up to 44 %) mayflies *Ephemerellidae* sp. (up to 34 %), *Caenidaes* sp. (up to 33 %), *Heptageneiidae* sp. (up to 33 %) and *Ephemeridae* sp. (up to 35 %). Finally, for damselflies *Zygoptera Coenagrionidae* sp. they ate mainly amphipods *H. azteca* (up to 31 %), mayflies *Ephemerellidae* sp. (up to 38 %), *Caenidaes* sp. (up to 33 %), *Heptageneiidae* sp. (up to 39 %) and *Ephemeridae* sp. (up to 33 %).

Discussion

So far, most current studies have focused on the pelagic food webs (Grey *et al.* 2000; Karlsson *et al.* 2003) and this study has the merit to consider the littoral food web which represents a key component of the functioning of aquatic systems (Schindler and Scheuerell 2002).

Potential food sources

The littoral benthic environment is complex (Wetzel 2001; Hecky and Hesslein 1995). Indeed, it can harbor several types of food sources with multiple origins such as POM, DOM and SOM (Meili 1992; Gu *et al.* 1994; Hecky and Hesslein 1995; Giorgio and France 1996; Grey *et al.* 2001; Vos *et al.* 2002; Macalady and Walton-Day 2009), primary producers (epilithon, macrophytes and epixylon) (Osmond *et al.* 1981; Hecky and Hesslein 1995; Wetzel 2001) and terrestrial detritus (Hecky and Hesslein 1995; Caraco and Cole 2004; Carpenter *et al.* 2005).

The POM has been removed from calculation of the linear mixing models because it does not inform us about the type of material that is eaten by organisms. It is not possible to say whether this source of carbon is allochthonous or authochthonous. Indeed, POM may be a mixture of several different carbon sources (Meili 1992; Wetzel 1995; Giorgio and France 1996; Grey *et al.* 2001). For instance, Giorgio and France (1996) showed that phytoplankton is frequently represented in the composition of POM and Fry and Sherr (1984) have shown that the isotopic signature of POM was related to phytoplankton productivity. In some lakes, POM is also composed of terrestrial detritus (Wetzel 1995) and the isotopic signature of the POM is the isotopic value of this terrestrial detritus (Jones *et al.* 1998). Grey *et al.* (2001) have found that in addition to terrestrial detritus and phytoplankton, POM also contains bacteria. Moreover, the isotopic value of the POM changes depending on its composition and the time of the year (Gu *et al.* 1994; Grey *et al.* 2001). In our study, $\delta^{13}C$ values of POM varied between -33.61 and -29.12 ‰ and were within the range reported by Giorgio and France (1996) (i.e., between -35 and -20 ‰).

Just as POM, SOM has been removed from the mixing model, since it does not

inform us about the nature of the OM. SOM can be a mixture of phytoplankton cells, macrophytes, organic matter of animal origin, bacteria and plant litter from land (Vos *et al.* 2002). Moreover, the degree of degradation of each component can also influence the results (Vos *et al.* 2002). Also, the SOM is the carbon source with the highest isotopic variability. This wide range of SOM is probably due to different origins of the OM and to different degrees of degradation.

DOM also has been removed from the mixing model. On the other hand, unlike the POM and SOM, the DOM was removed from calculations because its $\delta^{13}C$ values are much higher (-20.5 to -4.4 ‰) than those of other sources and consumers. These highly ^{13}C-enriched values compared to those reported by Jones *et al.* (1999) (^{13}C values varying between -28.5 and -25.3 ‰) suggest that the DOM in our lakes is of autochthonous origin (Jones *et al.* 1999).

$\delta^{13}C$ isotopic values in macrophytes are highly variable. These large variations in $\delta^{13}C$ among macrophytes may be due to the carbon source used, the bicarbonate (HCO^{3-}) or atmospheric carbon dioxide (CO_2) (Osmond *et al.* 1981; Keough *et al.* 1998). In fact, aquatic plants use the HCO^{3-} and CO_2 for photosynthesis, but the proportion of HCO^{3-} and CO_2 used by plants varies from one species to another and depends on the pH of the environnement (Allen and Spence 1981). Furthermore, both for plants of the same species and plants of differents species, the aerial leaves, floating leaves and submerged leaves may have different values of $\delta^{13}C$ (Osmond *et al.* 1981; Bunn and Boon 1993; Keough *et al.* 1996, 1998). Osmond *et al.* (1981) also found that $\delta^{13}C$ values would be higher in environments where there is little turbulence over more turbulent environments. Also, submerged leaves have a greater isotopic variability by site of sampling and the season of sampling, aerial leaves (Boon and Bunn 1994). In addition, macrophytes have leaves that grow underwater and then become floating leaves, and, therefore, have intermediate

isotopic signatures of between submerged plants and plants with aerial leaves (Keough *et al.* 1998). Finally, without mentioning of macrophytes with floating leaves or aerial leaves, LaZerte and Szalados (1982) reported that submerged macrophytes have a value of carbon isotope ratio higher than C_3 plants such as trees leaves. Although the position of leaves on macrophytes can increase the isotopic variation, during the sampling no distinction was made between submerged, floating or aerial macrophyte leaves. It is, therefore, not possible for us to separate the different values. On the other hand, living as well as dead macrophytes have $\delta^{13}C$ values higher than those of terrestrial leaf litter. Finally, the $\delta^{13}C$ values of macrophytes may vary whether they are alive or dead, and depending on the location, the season and the species (Bunn and Boon 1993).

Besides DOM, periphyton usually exhibited highly 13C-enriched values in our study excepted at sites with macrophytes in four lakes. These results agree well with those reported by Hadwen and Bunn (2005).

Based on our stable isotopic results, leaf-litter appeared to be a significant primary source of carbon for benthic primary consumers in six out of seven lakes, suggesting than carbon from the terrestrial environment may be a significant contributor to the littoral benthic food web. Also, the means of isotopic values in $\delta^{15}N$ of terrestrial leaf litter are the lowest value compared to the other sources. Although Herwig *et al.* (2004) have found $\delta^{15}N$ values higher than what we obtained, the values of C_3 plants they harvested had also the lowest value among the carbon sources they sampled. These results can be explained by the possible occurrence of fungi, which changes the level of nitrogen in leaves (Graça *et al.* 1993). In addition, although not mentioning any isotopic values, Friberg and Jacobsen (1994) reported that living macrophytes and algae have higher 15N values than fresh terrestrial leaves.

Trophic structure of lakes

In our oligotrophic lakes, the main source of carbon for macroinvetebrates scavengers and herbivorous is terrestrial leaf litter. This agrees with results reported by Cole *et al.* (2006). Indeed, in the four oligotrophic lakes they studied, they found that the main carbon source was particulate organic carbon of terrestrial origin (Cole *et al.* 2006). The extensive use of allochthonous carbon by macroinvertebrates could be due to the trophic state of the lake. Indeed, according to Cole *et al.* (2002) and Carpenter *et al.* (2005) the higher the trophic level of the lake, the lower the allochthonous carbon dependency.

The C_3 plants and macrophytes are hard to digest compared to algae such as periphyton (Mann 1988). The high levels of cellulose and lignin explain this. However, the presence of bacteria and fungi can overcome this problem since they are often able to digest these components (Mann 1988; Graça *et al.* 1993; Wright and Covich 2005). Also, with the decomposition process, the bacteria cause an enrichment of N (Mann 1988). The process of decomposition can vary according to different plant and depending on the types of bacteria or fungus present in the environment (Wright and Covich 2005). When invertebrates ingest terrestrial detritus, they also do ingest bacteria and fungi, which makes plant detritus more nutritious by increasing the protein content (Mann 1988; Wright and Covich 2005). The presence of these organisms could explain the high contribution of terrestrial detritus to the diet of benthic macroinvertebrates in our study.

Except for lakes Des Baies, Ferré and de l'Est, scavengers and herbivores likely did assimilate dead rather than living macrophytes. These results are consistent with those reported by several authors (Mann 1988; Newman 1991; Keough *et al.* 1996; Herwig *et al.* 2004). In fact, except for lakes des Baies, Ferré and de l'Est, dead macrophytes are the

second largest source of carbon for scavengers and herbivorous, when this carbon source occurs in the environment. Mann (1988) suggests that the grazing activity is directed towards decaying plants rather that living. Like terrestrial leaf litter, macrophytes contain cellulose and lignin. Having digested some of these components, the bacteria make dead macrophytes more digestible than living macrophytes by increasing the amount of nitrogen within the detritus, hence improving the nutritional value of macrophytes (Mann 1988).

Differences in the degree of consumption of macrophytes in lakes can be explained by several factors. The intensity of herbivory by invertebrates depends on macrophytes species, in addition, some sections of the plants would be preferred over others and consumtion of macrophytes is seasonnally variable (Lodge 1991; Jacobsen et Sand-Jensen 1992, 1995). Also, the consumption of macrophytes by invertebrates may vary depending by invertebrates species, but also among individuals keep the same species (Bunn and Boon 1993).

The periphyton was composed of epilithon and epixylon. At sites M, these two algal sources were equally used except by amphipods who did assimilate epixylon rather than epilithon. However, periphyton was, overall, not a significant source of carbon at these sites. At sites B, the epixylon was a more important carbon source than the epilithon for scavengers and herbivores. Nevertheless, the epilithon and the epixylon was not a carbon source as important as terrestrial detritus for scavengers and herbivorous. On the other hand, although they were consumed in lesser quantities than terrestrial detritus, different types of periphyton still represented between 19 and 47 % of the diet of macroinvertebrates at sites B and between 13 and 22 % at sites M. Algae have less fiber content and lignin than macrophytes and terrestrial plants (Mann 1988). It is perhaps for this reason that periphyton are preferentially consumed over macrophytes and terrestrial plants. Although periphyton consumption does occur in our studied lakes, this consumption is not as important as what

has been found by Hadwen and Bunn (2005). These authors found that periphyton contributes between 48 and 70 % to the diet of macroinvertebrates. However, Hadwen and Bunn (2005) did not distinguish between the various types of periphyton. Mulholland *et al.* (2000), meanwhile, found that mayflies *Heptageneiidae Stenonema* sp. fed on leaf litter and epilithon and mayflies *Baetidae Baetis* sp. fed primarily on epilithon. They also found that the amphipod *Gammarus minus* fed more on epixylon than on leaf litter. Like Mulholland *et al.* (2000), we found that epixylon is an important food source for amphipods. Also, Herwig *et al.* (2004) found the same result, but only during some seasons. The results of these studies suggest that insects and crustaceans, they studied, are primarily herbivores. Conversely, in our study, insects and crustaceans were rather detritivores. Our study did not include epiphyton. It would have been interesting to include this primary producer component in our study, since several studies have found this carbon source as important for the diet of many macroinvertebrates (Bunn and Boon 1993, James *et al.* 2000a; Herwig *et al.* 2004).

In some lakes (lake Neigette, lake Ferré and lake Macpès), scavengers have high values $\delta^{15}N$. These high $\delta^{15}N$ values could be explained by the occurrence of bacteria and fungi in their food sources (Mann 1988; Graça *et al.* 1993; Wright and Covich 2005). Indeed, since bacteria and fungi decompose litter and terrestrial macrophytes died (Mann 1988; Graça *et al.* 1993; Wright and Covich 2005), so we can suppose that the high values $\delta^{15}N$ partly due to the ingestion of these microorganisms. In addition, during the process of decomposition by bacteria, a N enrichment occurs (Mann 1988). Although the $\delta^{15}N$ values of scavengers of three lakes (lake Neigette, lake Ferré and lake Macpès) are high (3.21 to 6.67 ‰), they correspond to the values reported by Beaudoin *et al.* 2001, (5.2 to 6.6 ‰) for amphidods in lakes they studied. Also, insects with trophic levels of two and three have $\delta^{15}N$ values higher than those of scavengers and herbivorous. $\delta^{15}N$ enrichment varies from about 2-4 ‰ per trophic level (Minagawa and Wada 1984; Ehleringer *et al.* 1986; Peterson and Fry 1987; Keough *et al.* 1996), this enrichment can vary depending on the age of the

organism, the size and nutritional status (Minagawa and Wada 1984; Peterson and Fry 1987; Keough *et al.* 1996).

Scavengers occurring in our lakes consume mainly terrestrial leaf litter, but also macrophytes and periphyton. These results are consistent with those of Friberg and Jacobsen (1994), who found that scavengers supplemented their diet with macrophytes and algae. Also, Solomon *et al.* (2011) found these food sources are important for the food web, but this importance varies in function of organisms and ecosystem properties. Moreover, for scavengers, herbivores, omnivores and carnivores, isotopic values of differents families of invertebrates are quite variable from one lake to another. Since we did not identify our macroinvertebrates at the species level, it is possible that we have brought together two species with different feeding behavior (Merrit and Cummins 1996). Pooling different species together could explain why the results of mixing models may differ from one lake to another, as it is the case for the family caddisflies *Leptoceridae* sp. On the other hand, the isotopic value of the same species may change depending on the lake, according to season, depending on the depth and depending on the amount of DOC and dissolved inorganic carbon (DIC) present in the water column (Premke *et al.* 2010; Grey *et al.* 2004b; James *et al.* 2000a). A small variation of DOC was observed in lakes and this could partly explain the isotopic variation we observed. Moreover, as we have already mentioned, the enrichment $\delta^{15}N$ may vary depending on the age of the organism, its size and the nutritional status (Mingawa and Wada 1984; Peterson and Fry 1987; Keough *et al.* 1996). Finally, there is also the possibility that we did not sample all of the possible food sources for each species.

Trophic position

The trophic position of macroinvertebrates was calculated using $\delta^{15}N$ values of periphyton as primary producer and $\delta^{15}N$ values of gastropods sp. as primary consumer (Post 2002). These calculations showed that in our lakes, there are three trophic levels

among littoral benthic invertebrates. At the first level we find scavengers and herbivorous: amphipods, mayflies *Caenidae* sp., *Ephemerellidae* sp., *Heptageneiidae* sp., *Ephemeridae* sp. Omnivores and carnivores, midges *Chironomidae* sp. dragonflies *Anisoptera Libellulidae* sp. and damselflies *Zygoptera Coenagrionidae* sp. occupy the second trophic level and caddisflies *Leptoceridae* sp. that are only found in the third trophic level. On the other hand, the caddisflies *Leptoceridae* sp. have a fairly high standard deviation (0.99). As the identification was not made at the species level, it is possible that some caddisflies rather be included in the second trophic level. These results are consistent with those of Vander Zanden and Rasmussen (1999) and Anderson and Cabana (2007).

Conclusion

In conclusion, primary benthic consumers of the studied lakes are primarily feeding on terrestrial detritus, so on allochthonous carbon. Terrestrial inputs are likely very important for the benthic food web of these lakes. Nevertheless, the consumption of periphyton also is important in environments devoid of macrophytes. When macrophytes are present, they are mainly assimilated by invertebrates, in the detrital form. As for omnivorous and carnivorous, diets vary greatly depending on families and on lakes. However, the stable isotopic signatures of omnivorous and carnivorous families are less well defined. It is possible that we did not sample all the prey of omnivorous and carnivorous, so this could explain the results obtained for carnivorous and omnivorous. In addition, identification to the species of different families could allow an increased accuracy results obtained with the mixing models. Indeed, as the identification was not done until species, it is possible that we have grouped species with different feeding regimes. In our lakes, there were three trophic levels among benthic invertebrates.

Overall, these results show the importance of terrestrial detritus for the littoral benthic food web and highlight the tight nature of the coupling between lakes and their surrounding

terrestrial habitats.

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Table 1. Physico-chemical characteristics of the seven studied lakes. pH, conductivity, temperature, chl *a*, total phosphorus (TP), dissolved organic carbon (DOC), dissolved inorganic phosphorus (DIP) and dissolved inorganic nitrogen (DIN) are reported as means (SD) for the sites with (M) and without (B) macrophytes, and means (SD) for secchi depth for lakes.

Lake	pH	Conductivity (µS/cm)	Temperature °C	Chl *a* (mg/m^{-3})	Total phosphorus (µg/L)	DOC (mg/L)	DIP (µmol/L)	DIN (µmol/L)	Secchi depth (m)
Noir M	6.5 (0.31)	350 (4)	18.71 (0.86)	2.72 (0.36)	6.11 (0.4)	4.38 (0.19)	0.05 (0.01)	0.09 (0.04)	2.22 (0.18)
Noir B	6.96 (0.28)	326 (59.86)	19.85 (0.88)	2.19 (0.32)	5.25 (1.1)	4.00 (0.02)	0.06 (0.05)	0.15 (0.1)	
Neigette M	7.9 (0.88)	502.67 (11.06)	19.15 (0.34)	6.72 (0.91)	5.58 (0.54)	6.49 (1.26)	0.05 (0.02)	13.18 (0.33)	2.25 (0)
Neigette B	8.55 (0.05)	506 (5.29)	19.5 (0.16)	6.88 (0.27)	4.92 (1.25)	5.78 (0.12)	0.05 (0.01)	14.40 (1.37)	
Des Baies M	8.1 (0.13)	202 (20)	17.94 (0.2)	0.88 (0.3)	4.93 (1.26)	6.32 (3.14)	0.02 (0.004)	0.05 (0.01)	7.75 (0)
Des Baies B	8.05 (0.05)	249.67 (80.09)	17.48 (1.15)	0.93 (0.21)	5.57 (1.25)	3.09 (2.7)	0.03 (0.003)	0.06 (0.01)	
Ferré M	8.88 (0.14)	376 (8)	20.1 (0.1)	3.77 (0.25)	3.41 (0.82)	4.32 (0.08)	0.16 (0.20)	6.82 (0.85)	4.00 (0)
Ferré B	8.76 (0.14)	376 (2)	19.6 (0.06)	2.37 (1.61)	20.5 (10.06)	5.02 (0.62)	0.04 (0.01)	7.41 (0.67)	
De l'Est M	8.59 (0.03)	352.33 (37.98)	19.58 (0.4)	2.66 (0.19)	6.47 (0.56)	3.21 (0.13)	0.03 (0.02)	0.06 (0.05)	3.75 (0.35)
De l'Est B	8.65 (0.06)	294 (25.51)	19.42 (0.28)	2.5 (0.47)	5.90 (0.23)	3.24 (0.16)	0.01 (0.01)	0.03 (0.02)	
Macpès M	8.12 (0.09)	176.33 (0.58)	19.64 (0.33)	3.08 (0.08)	4.92 (1.21)	6.39 (0.72)	0.01 (0.01)	4.72 (0.54)	3.50 (0)
Macpès B	8.27 (0.03)	177 (0)	19.89 (0.49)	2.92 (0.27)	5.49 (1.02)	5.97 (0.05)	0.01 (0.01)	4.42 (0.59)	
Petit Touradi M	7.58 (0.14)	102.33 (0.58)	21.11 (0.96)	2.6 (0.71)	6.97 (1.27)	5.51 (0.33)	-0.01 (0.003)	0.01 (0.002)	3.25 (0.35)
Petit Touradi B	7.7 (0.06)	102.33 (0.58)	20.82 (0.24)	2.91 (0.76)	5.12 (0.63)	3.89 (2.92)	-0.01 (0.004)	0.02 (0.01)	

Table 2. Trophic-position estimates of consumers in the seven lakes at sites with (M) and without (B) macrophytes.

Lakes Consummers	Noir M	Neigette M	Neigette B	Des Baies M	Des Baies B	Ferré M	Ferré B	Macpès M	Petit Touradi M	Mean (SD)
Hyalella azteca	1,85	1,78	1,61	1,59	1,74	1,59	1,59	1,66	1,90	1,70 (0,12)
Caenidae	1,83	1,84	1,81	1,69	1,66	1,76	n/a	1,82	1,90	1,79 (0,08)
Heptageneiidae	n/a	n/a	1,59	1,86	2,06	1,76	1,77	2,33	2,79	2,02 (0,41)
Ephemeridae	n/a	n/a	n/a	1,69	1,83	2,11	2,35	n/a	2,23	2,04 (0,27)
Ephemerellidae	1,92	1,83	1,51	1,54	1,11	1,61	1,49	1,57	2,08	1,63 (0,28)
Chironomidae	2,26	2,13	1,88	n/a	2,58	2,17	2,22	2,36	n/a	2,23 (0,21)
Libellulidae	n/a	2,26	2,26	2,11	2,45	2,20	n/a	n/a	2,43	2,28 (0,13)
Coenagrionidae	2,81	2,74	2,56	2,82	2,73	2,66	2,78	3,20	2,84	2,79 (0,17)
Leptoceridae	n/a	3,79	3,20	2,30	5,37	3,39	2,64	3,24	n/a	3,42 (0,99)

Table 3. Bayesian mixing model (SIAR) results for consumers at sites with macrophytes (M) in seven lakes. Values represent the mean and the 1st to 99th percentile range of potential contribution in percentage.

Lake		Living macrophytes	Dead macrophytes	Epilithon	Epixylon	Leaf litter	*Hyalella azteca*	*Caenidae*	*Heptageneiidae*	*Hydracarian*	*Ephemeridae*	*Ephemerellidae*	*Chironomidae*	*Coenagrionidae*	*Libellulidae*
Noir	*Hyalella azteca*	19; 0-37	23; 8-37	17; 0-35	18; 0-36	22; 0.06-43	-	-	n/a	-	n/a	-	-	-	n/a
	Caenidae	19; 0-37	23; 7.8-37	18; 0-36	18; 0-36	22; 0.05-41	-	-	n/a	-	n/a	-	-	-	n/a
	Ephemerellidae	19; 0-37	21; 3.2-35	19; 0-37	20; 0.1-37	21; 0-39	-	-	n/a	-	n/a	-	-	-	n/a
	Chironomidae	-	-	-	-	27; 0-51	25; 0-49	24; 0-48	n/a	-	n/a	23; 0-48	-	-	n/a
	Coenagrionidae	-	-	-	-	-	28; 1.4-53	33; 0.7-61	n/a	-	n/a	38; 6.8-66	-	-	n/a
Neigette	*Hyalella azteca*	18; 0-36	22; 0-43	18; 0-37	18; 0-37	24; 0.7-43	-	-	n/a	-	n/a	-	-	-	-
	Caenidae	18;0-37	22; 0-42	19; 0-37	19; 0-18	23; 0.4-43	-	-	n/a	-	n/a	-	-	-	-
	Ephemerellidae	20; 0-39	20; 0-40	20; 0-39	20; 0-39	20; 0-37	-	-	n/a	-	n/a	-	-	-	-
	Leptoceridae	-	-	-	-	-	24; 0-48	25; 0-49	n/a	-	n/a	25; 0-48	26; 0-50	-	-
	Chironomidae	-	23; 0.07-43	-	-	26; 2.5-45	16; 0-35	18; 0-37	n/a	-	n/a	17; 0-35	-	-	-
	Coenagrionidae	-	-	-	-	-	28; 1.2-50	26; 0-49	n/a	-	n/a	27; 0.06-51	20; 0-39	-	-
	Libellulidae	-	-	-	-	-	30; 0.8-55	24; 0-47	n/a	-	n/a	27; 0-53	19; 0-41	-	-
Des Baies	*Hyalella azteca*	19; 0-38	14; 0-33	18; 0-38	22; 0-43	26; 0.8-49	-	-	-	-	-	-	n/a	-	-
	Caenidae	20; 0-39	19; 0-38	20; 0-39	20; 0-40	20; 0-39	-	-	-	-	-	-	n/a	-	-
	Heptageneiidae	20; 0-39	20; 0-39	20; 0-39	20; 0-39	20; 0-39	-	-	-	-	-	-	n/a	-	-
	Ephemerellidae	20; 0-40	18; 0-37	20; 0-39	21; 0-40	21; 0-41	-	-	-	-	-	-	n/a	-	-
	Ephemeridae	-	-	-	21; 0-41	21; 0-41	21; 0-40	17; 0-35	-	-	-	19; 0-39	n/a	-	-
	Leptoceridae	19; 0-37	-	21; 0-40	20; 0-39	-	20; 0-40	-	-	-	20; 0-39	-	n/a	-	-
	Coenagrionidae	-	-	-	-	-	-	31; 0-59	39; 1.0-73	-	-	30; 0-57	n/a	-	-
	Libellulidae	-	-	-	-	-	26; 0-49	-	22; 0-44	-	24; 0-48	28; 0-53	n/a	-	-

Lakes		Living macrophytes	Dead macrophytes	Epilithon	Epixylon	Leaf litter	*Hyalella azteca*	*Caenidae*	*Heptageneiidae*	*Hydracarian*	*Ephemeridae*	*Ephemerellidae*	*Chironomidae*	*Coenagrionidae*	*Libellulidae*
Ferré	*Hyalella azteca*	19; 0-37	19; 0-39	15; 0-35	19; 0-39	28; 1.1-53	-	-	-	-	-	-	-	-	-
	Caenidae	17; 0-37	19; 0-39	16; 0-35	20; 0-39	28; 2.2-49	-	-	-	-	-	-	-	-	-
	Heptageneiidae	19; 0-39	19; 0-39	20; 0-40	20; 0-40	21; 0-40	-	-	-	-	-	-	-	-	-
	Ephemerellidae	15; 0-34	18; 0-38	13; 0-32	19; 0-39	35; 7.1-61	-	-	-	-	-	-	-	-	-
	Ephemeridae	-	15; 0-31	-	-	23; 3.9-38	14; 0-30	15; 0-31	15; 0-31	-	-	17; 0-34	-	-	-
	Leptoceridae	-	-	-	-	-	-	29; 0-59	-	-	35; 0-68	37; 0.4-69	-	-	-
	Chironomidae	17; 0-32	-	-	-	21; 2.5-36	13; 0-28	16; 0-32	16; 0-33	-	-	16; 0-31	-	-	-
	Coenagrionidae	-	-	-	-	-	17; 0-33	20; 0-39	18; 0-37	-	20; 0-38	25; 0.3-47	-	-	-
	Libellulidae	-	-	-	-	-	21; 0-43	26; 0-51	26; 0-49	-	-	26; 0.1-49	-	-	-
De l'Est	*Hyalella azteca*	20; 0-38	20; 0-39	20; 0-40	19; 0-39	21; 0-41	-	-	-	-	n/a	-	n/a	-	-
	Caenidae	20; 0-39	16; 0-35	19; 0-38	18; 0-38	27; 1.3-50	-	-	-	-	n/a	-	n/a	-	-
	Heptageneiidae	20; 0-39	20; 0-39	20; 0-39	20; 0-40	21; 0-39	-	-	-	-	n/a	-	n/a	-	-
	Ephemerellidae	20; 0-39	16; 0-35	19; 0-38	19; 0-38	27; 0.8-50	-	-	-	-	n/a	-	n/a	-	-
	Leptoceridae	-	-	-	-	-	-	25; 0-48	25; 0-48	27; 0.1-50	n/a	24; 0-47	n/a	-	-
	Coenagrionidae	-	-	-	-	-	31; 8.5-53	26; 0-50	19; 0-38	-	n/a	23; 0.05-44	n/a	-	-
	Libellulidae	-	-	-	-	-	44; 3.5-82	30; 0-60	-	-	n/a	27; 0-56	n/a	-	-
Macpès	*Hyalella azteca*	15; 0-32	19; 0-37	16; 0-35	20; 0.05-38	30; 9-51	-	-	-	-	n/a	-	-	-	n/a
	Caenidae	20; 0-38	20; 0-39	20; 0-38	20; 0-39	20; 0-39	-	-	-	-	n/a	-	-	-	n/a
	Heptageneiidae	20; 0-39	24; 0.03-45	19; 0-36	22; 0.1-42	18; 0-38	-	-	-	-	n/a	-	-	-	n/a
	Ephemerellidae	19; 0-38	20; 0-38	20; 0-39	20; 0-39	21; 0.09-40	-	-	-	-	n/a	-	-	-	n/a
	Leptoceridae	-	-	-	-	-	-	-	-	25; 0-49	n/a	25; 0-49	25; 0-49	24; 0-49	n/a
	Chironomidae	-	33; 0-64	-	-	32; 0-63	-	-	-	-	n/a	35; 0-67	-	-	n/a
	Coenagrionidae	-	-	-	-	-	-	-	27; 0.8-50	21; 0-41	n/a	27; 0.9-49	25; 0-46	-	n/a

Lakes		Living macrophytes	Dead macrophytes	Epilithon	Epixylon	Leaf litter	*Hyalella azteca*	*Caenidae*	*Heptageneiidae*	*Hydracarian*	*Ephemeridae*	*Ephemerellidae*	*Chironomidae*	*Coenagrionidae*	*Libellulidae*
Petit Touradi	*Hyalella azteca*	15; 0-33	21; 0-41	18; 0-36	20; 0.1-39	26; 0.9-46	-	-	-	-	-	-	n/a	-	-
	Caenidae	13; 0-32	18; 0-37	21; 0-40	22; 0-42	27; 0.4-51	-	-	-	-	-	-	n/a	-	-
	Heptageneiidae	12; 0-29	19; 0-37	19; 0-39	21; 0-41	29; 0.9-54	-	-	-	-	-	-	n/a	-	-
	Ephemerellidae	19; 0-38	20; 0-38	21; 0-40	20; 0-39	20; 0-39	-	-	-	-	-	-	n/a	-	-
	Ephemeridae	-	-	-	-	29; 0.03-55	21; 0-41	24; 0-47	-	-	-	27; 0.07-50	n/a	-	-
	Coenagrionidae	-	-	-	-	-	-	25; 0-49	-	-	25; 0-48	25; 0-49	n/a	-	24; 0-48
	Libellulidae	-	-	-	-	-	-	32; 0.5-61	-	-	35; 1.5-63	33; 4.0-56	n/a	-	-

Table 4. Bayesian mixing model (SIAR) results for consumers at sites without macrophytes (B) in the seven lakes. Values represent the mean and the 1st to 99th percentile range of potential contribution.

Lakes		Epilithon	Epixylon	Leaf litter	*Hyalella azteca*	*Caenidae*	*Heptageneiidae*	*Leptoceridae*	*Ephemeridae*	*Ephemerellidae*	*Chironomidae*	*Libellulidae*
Noir	*Hyalella azteca*	27; 0-57	35; 1.3-63	38; 2.1-69	-	-	-	-	n/a	-	-	-
	Caenidae	27; 0-55	33; 0-64	41; 2.8-75	-	-	-	-	n/a	-	-	-
	Heptageneiidae	35; 0.9-65	31; 0-61	34; 0.2-64	-	-	-	-	n/a	-	-	-
	Ephemerellidae	26; 0-54	30; 0-60	44; 5.2-79	-	-	-	-	n/a	-	-	-
	Leptoceridae	20; 0-42	28; 0.3-53	29; 2.0-51	22; 0.03-43	-	-	-	n/a	-	-	-
	Chironomidae	-	-	46; 11.0-79	-	32; 0-61	-	-	n/a	22; 0-49	-	-
	Coenagrionidae	-	-	-	-	31; 1.8-56	24; 0-46	-	n/a	23; 0.09-44	-	21; 0.2-40
	Libellulidae	-	-	-	-	33; 0-65	33; 0-64	-	n/a	34; 0-66	-	-
Neigette	*Hyalella azteca*	29; 0-57	36; 2.8- 65	35; 4.8-61	-	-	-	-	n/a	-	-	-
	Caenidae	29; 0-56	47; 13.7-82	24; 1.2-46	-	-	-	-	n/a	-	-	-
	Heptageneiidae	28; 0-58	34; 0.8-64	38; 2.4-72	-	-	-	-	n/a	-	-	-
	Ephemerellidae	29; 0-57	35; 2.1-64	36; 7.4-62	-	-	-	-	n/a	-	-	-
	Leptoceridae	-	-	-	20; 0-38	20; 0-40	20; 0-40	-	n/a	20; 0-39	20; 0-39	-
	Chironomidae	-	-	27; 2.3-45	22; 0-44	-	23; 0-46	-	n/a	27; 0.4-52	-	-
	Coenagrionidae	-	-	-	18; 0-37	17; 0-36	28; 0.8-54	-	n/a	-	18; 0-37	-
	Libellulidae	-	-	-	20; 0-39	19; 0-38	21; 0-40	-	n/a	21; 0-40	19; 0-38	-
Des Baies	*Hyalella azteca*	27; 0-54	32; 0.4-60	41; 3.3-74	-	-	-	-	-	-	-	-
	Caenidae	29; 0-59	30; 0-60	41; 2.1-79	-	-	-	-	-	-	-	-
	Heptageneiidae	28; 0-57	29; 0-59	43; 4.2-77	-	-	-	-	-	-	-	-
	Ephemerellidae	27; 0-57	28; 0-57	45; 5.2-83	-	-	-	-	-	-	-	-
	Ephemeridae	-	-	33; 0-65	-	33; 0-65	-	-	-	34; 0-65	-	-
	Leptoceridae	-	-	-	-	34; 0-65	32; 0-62	-	34; 0-66	-	-	-
	Chironomidae	-	-	16; 0-31	19; 0.05-36	17; 0-33	14; 0-28	-	18; 0-34	16; 0-31	-	-
	Coenagrionidae	-	-	-	22; 0.1-41	20; 0-39	18; 0-35	-	21; 0-37	19; 0-37	-	-
	Libellulidae	-	-	-	35; 0.08-66	32; 0-62	33; 0-64	-	33; 0-64	-	-	-

Lakes		Epilithon	Epixylon	Leaf litter	*Hyalella azteca*	*Caenidae*	*Heptageneiidae*	*Leptoceridae*	*Ephemeridae*	*Ephemerellidae*	*Chironomidae*	*Libellulidae*
Ferré	*Hyalella azteca*	26; 0-52	29; 0.2- 54	45; 18-73	-	n/a	-	-	-	-	-	n/a
	Heptageneiidae	26; 0-54	32; 0-59	42; 6.7-77	-	n/a	-	-	-	-	-	n/a
	Ephemerellidae	19; 0-45	24; 0.3-46	58; 33-87		n/a	-	-	-	-	-	n/a
	Ephemeridae	-	-	25; 6.5-42	-	n/a	24; 0-46	-	-	26; 0.3-49	25; 0.9-45	n/a
	Leptoceridae	-	-	26; 0-52	-	n/a	37; 0.9-72	-	36; 1.0-66	-	-	n/a
	Chironomidae	-	-	24; 5.2-41	20; 0-39	n/a	28; 1.6-50	-	-	28; 0.5-52	-	n/a
	Coenagrionidae	-	-	-	-	n/a	33; 0-64	-	33; 0-64	34; 0-66	-	n/a
De l'Est	*Hyalella azteca*	22; 0-51	25; 0-51	53; 21.3-89	-	-	-	n/a	-	-	-	-
	Caenidae	27; 0-55	28; 0-55	44; 10.8-81	-	-	-	n/a	-	-	-	-
	Heptageneiidae	33; 0-65	33; 0-64	34; 0-66	-	-	-	n/a	-	-	-	-
	Ephemerellidae	27; 0-55	27; 0-54	46; 12.3-85	-	-	-	n/a	-	-	-	-
	Ephemeridae	-	-	26; 0-49	25; 0-49	25; 0-49	-	n/a	-	25; 0-48	-	-
	Chironomidae	-	-	22; 0.2-41	18; 0-37	21; 0-41	17; 0-36	n/a	-	21; 0-40	-	-
	Libellulidae	-	-	-	34; 0-66	33; 0-65	-	n/a	-	33; 0-64	-	-
Macpès	*Hyalella azteca*	31; 0-60	27; 0-51	43; 10.1-72	-	-	-	-	-	-	-	n/a
	Caenidae	38; 3.0-68	41; 4.9-74	22; 0-48	-	-	-	-	-	-	-	n/a
	Heptageneiidae	37; 1.4-68	31;0.3-58	32; 0.4-61	-	-	-	-	-	-	-	n/a
	Ephemerellidae	33; 1.6-60	32; 4.5-56	35; 8.7-58				-				n/a
	Ephemeridae	19; 0-37	21; 0-40	19; 1.5-33	21; 0.3-39	-	-	-	-	20; 0.3-37	-	n/a
	Leptoceridae	-	-	-	36; 1.1-69	-	-	-	33; 0-63	-	31; 0-61	n/a
	Chironomidae	25; 0-48	24; 0-47	25; 0-48	26; 0.3-50	-	-	-	-	-	-	n/a
	Coenagrionidae	-	-	-	-	25; 0-48	-	26; 0-49	26; 0-49	-	24; 0-48	n/a
Petit Touradi	*Hyalella azteca*	31; 0-63	27; 0-58	42; 2.0-82	-	-	-	n/a	-	n/a	-	n/a
	Caenidae	33; 0-64	29; 0-59	39; 0.02 75	-	-	-	n/a	-	n/a	-	n/a
	Heptageneiidae	21; 0-51	24; 0-55	54; 12.9-97	-	-	-	n/a	-	n/a	-	n/a
	Ephemeridae	-	-	54; 16.9-91	21; 0-48	25; 0-55	-	n/a	-	n/a	-	n/a
	Chironomidae	-	-	26; 0-49	25; 0-49	25; 0-50	-	n/a	24; 0-49	n/a	-	n/a
	Coenagrionidae	-	-	-	21; 0-40	21; 0-41	18; 0-38	n/a	19; 0-38	n/a	21; 0-40	n/a

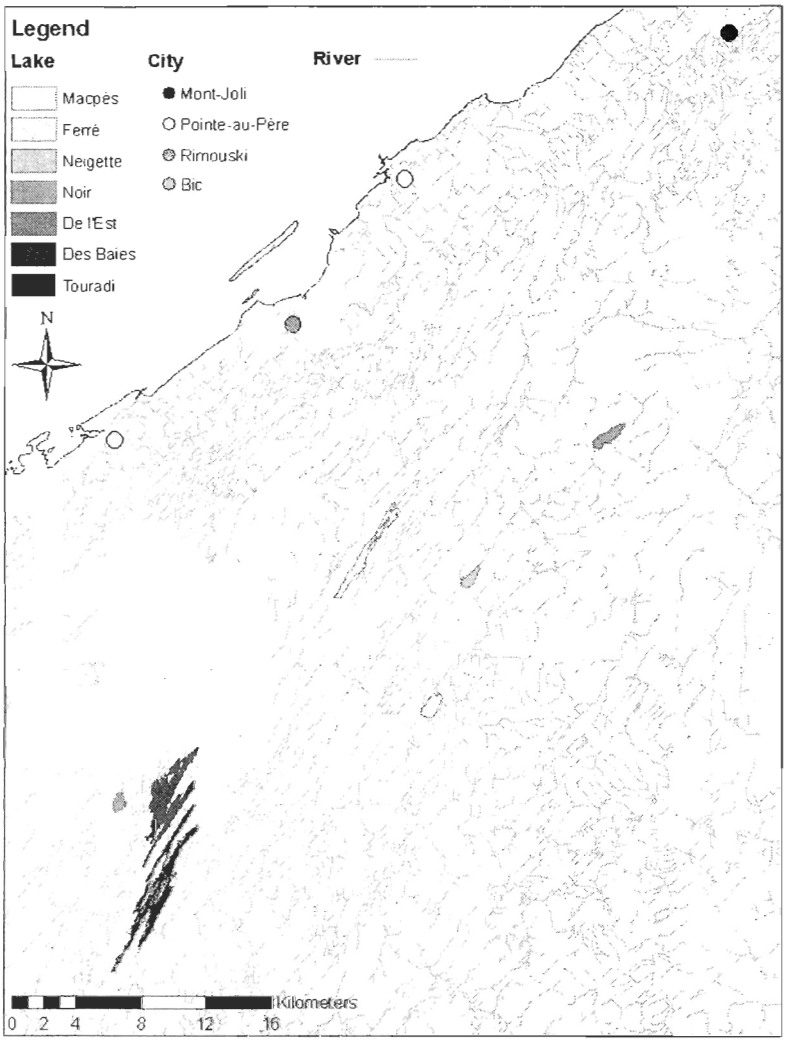

Figure 1: Map of the seven lakes sampled for the study in the Bas-St-Laurent region

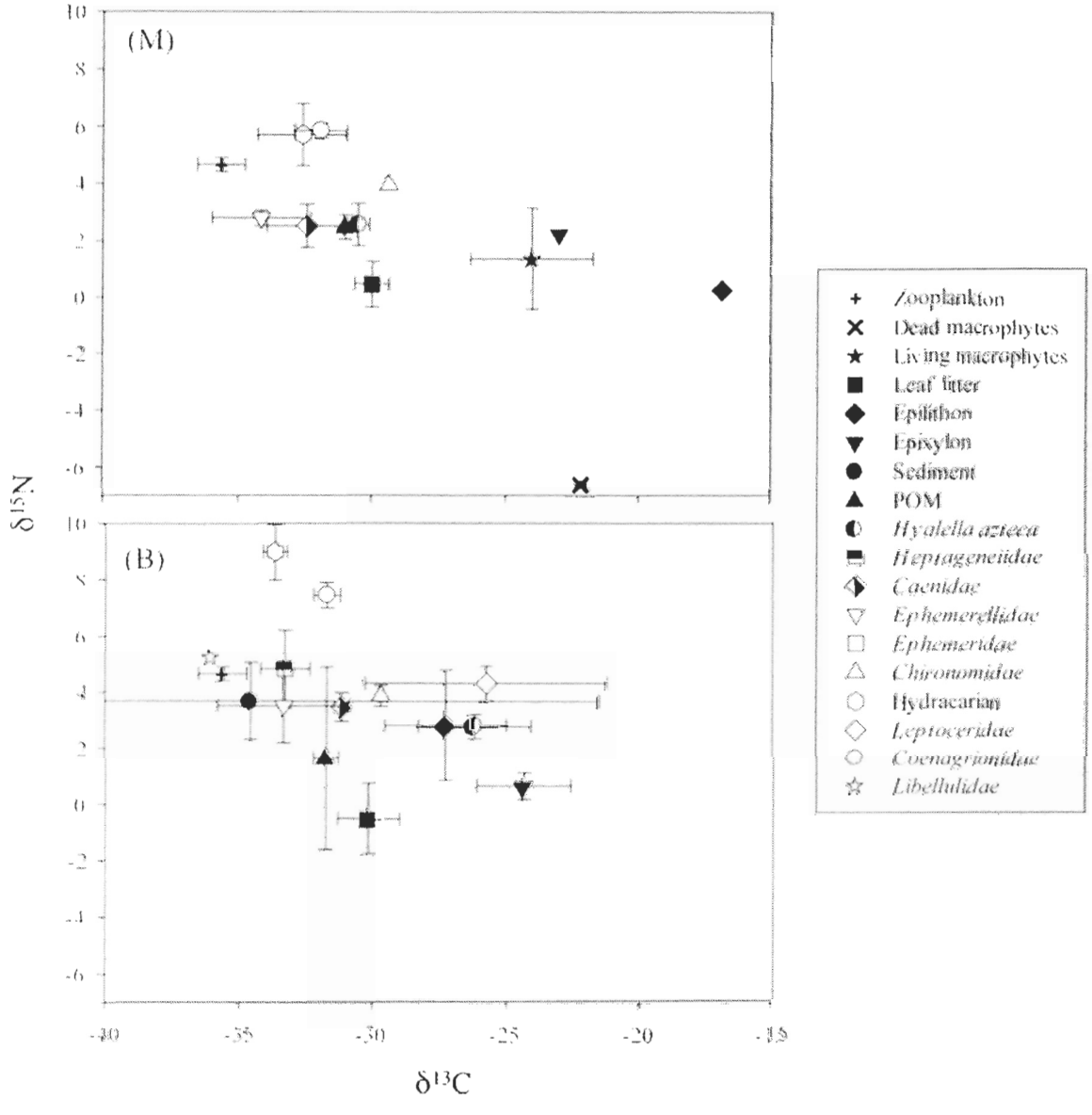

Figure 2. $\delta^{13}C$ and $\delta^{15}N$ of potential food sources and consumers for the lake Noir at sites with (M) and without (B) macrophytes. Error bars represent the mean ± SD.

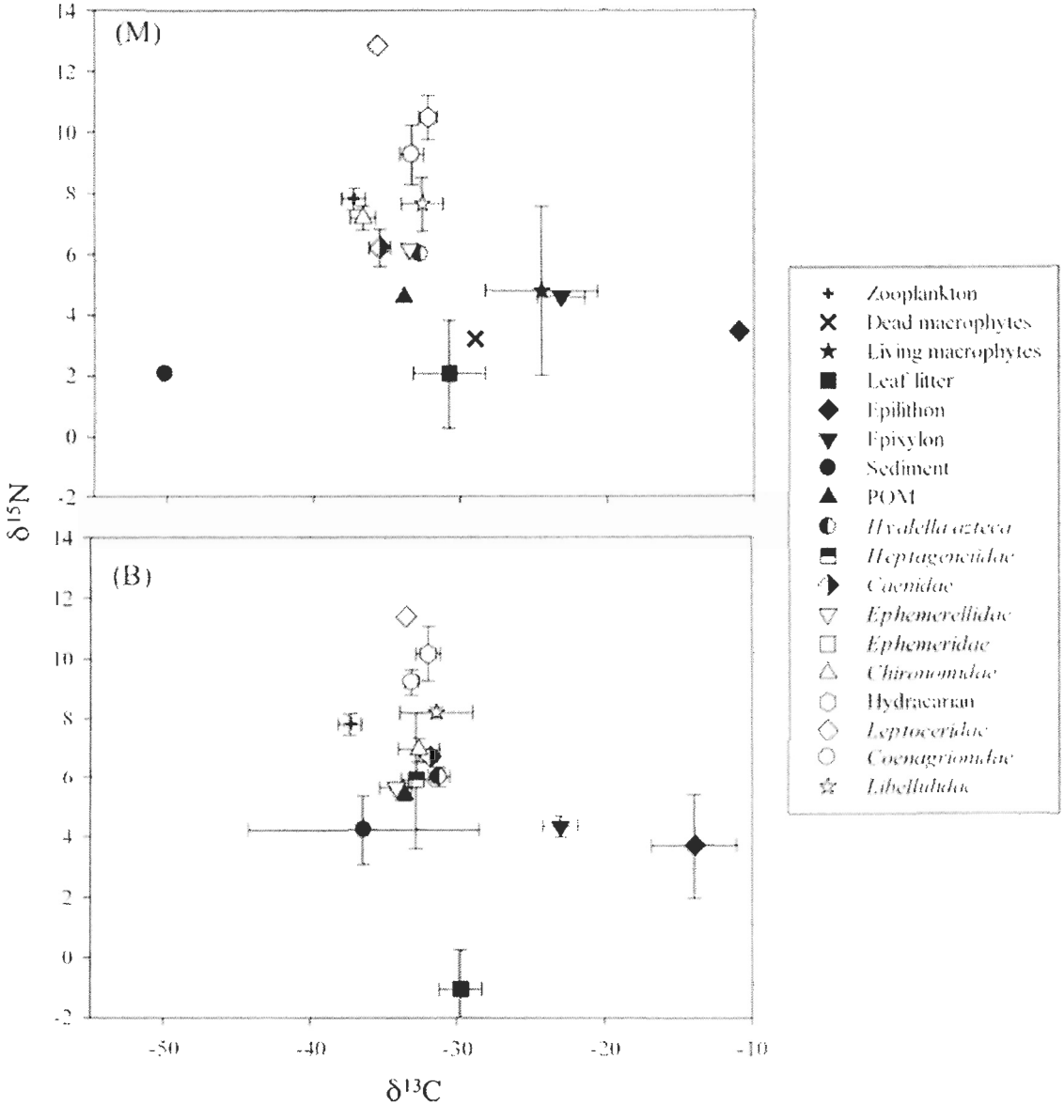

Figure 3. $\delta^{13}C$ and $\delta^{15}N$ of potential food sources and consumers for the lake Neigette at sites with (M) and without (B) macrophytes. Error bars represent the mean ± SD.

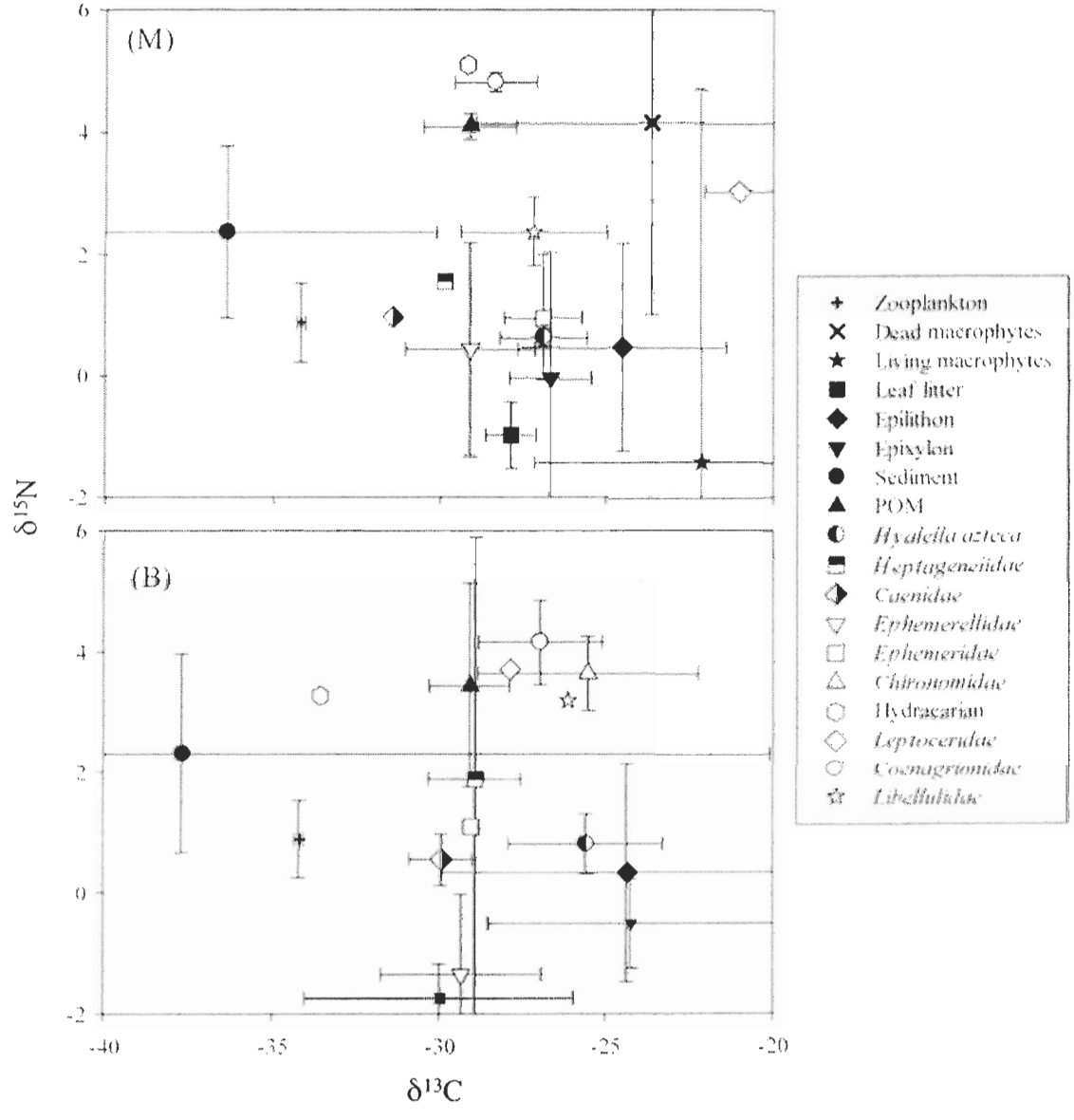

Figure 4. $\delta^{13}C$ and $\delta^{15}N$ of potential food sources and consumers for the lake Des Baies at sites with (M) and without (B) macrophytes. Error bars represent the mean ± SD.

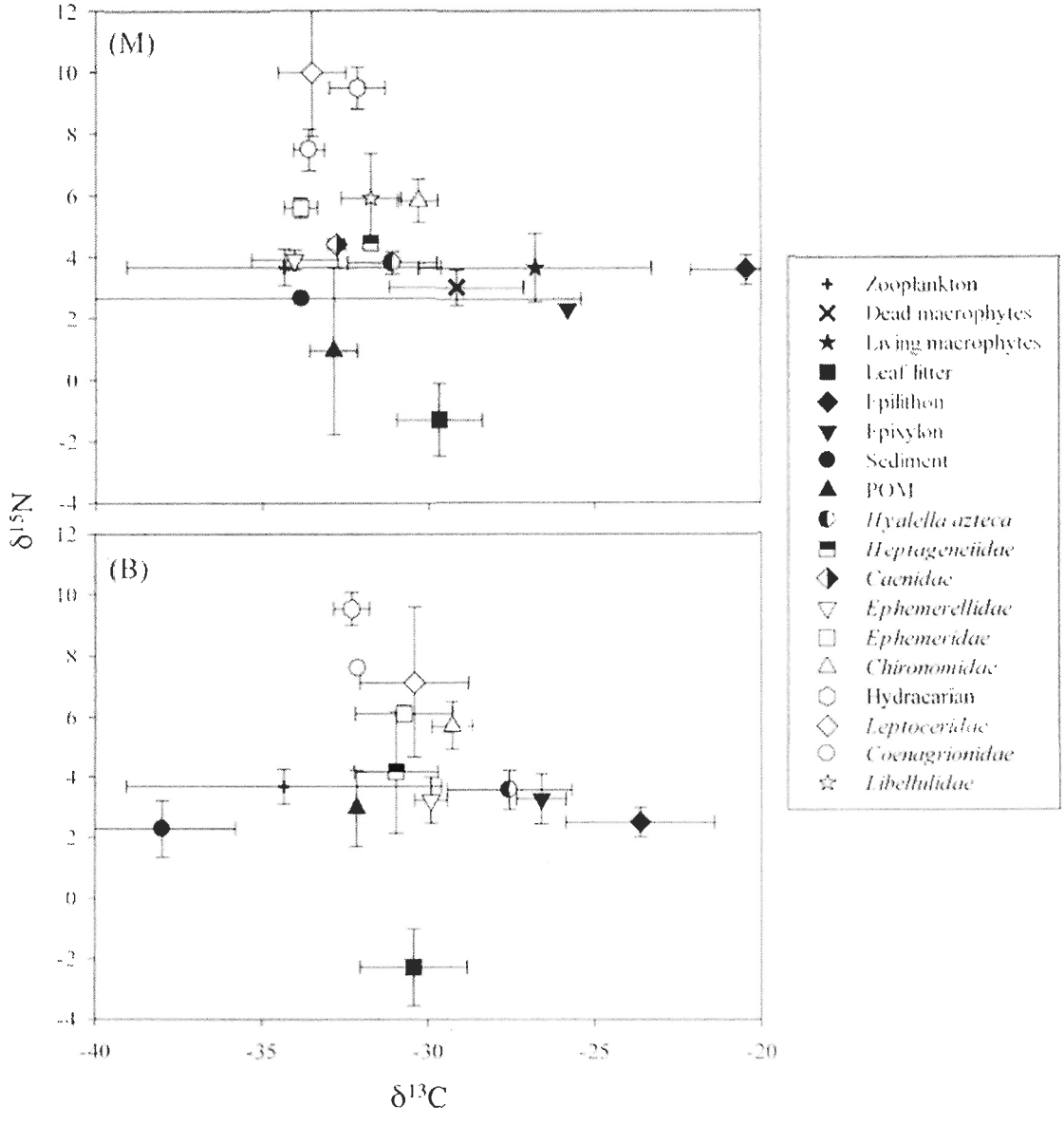

Figure 5. $\delta^{13}C$ and $\delta^{15}N$ of potential food sources and consumers for the lake Ferré at sites with (M) and without (B) macrophytes. Error bars represent the mean ± SD.

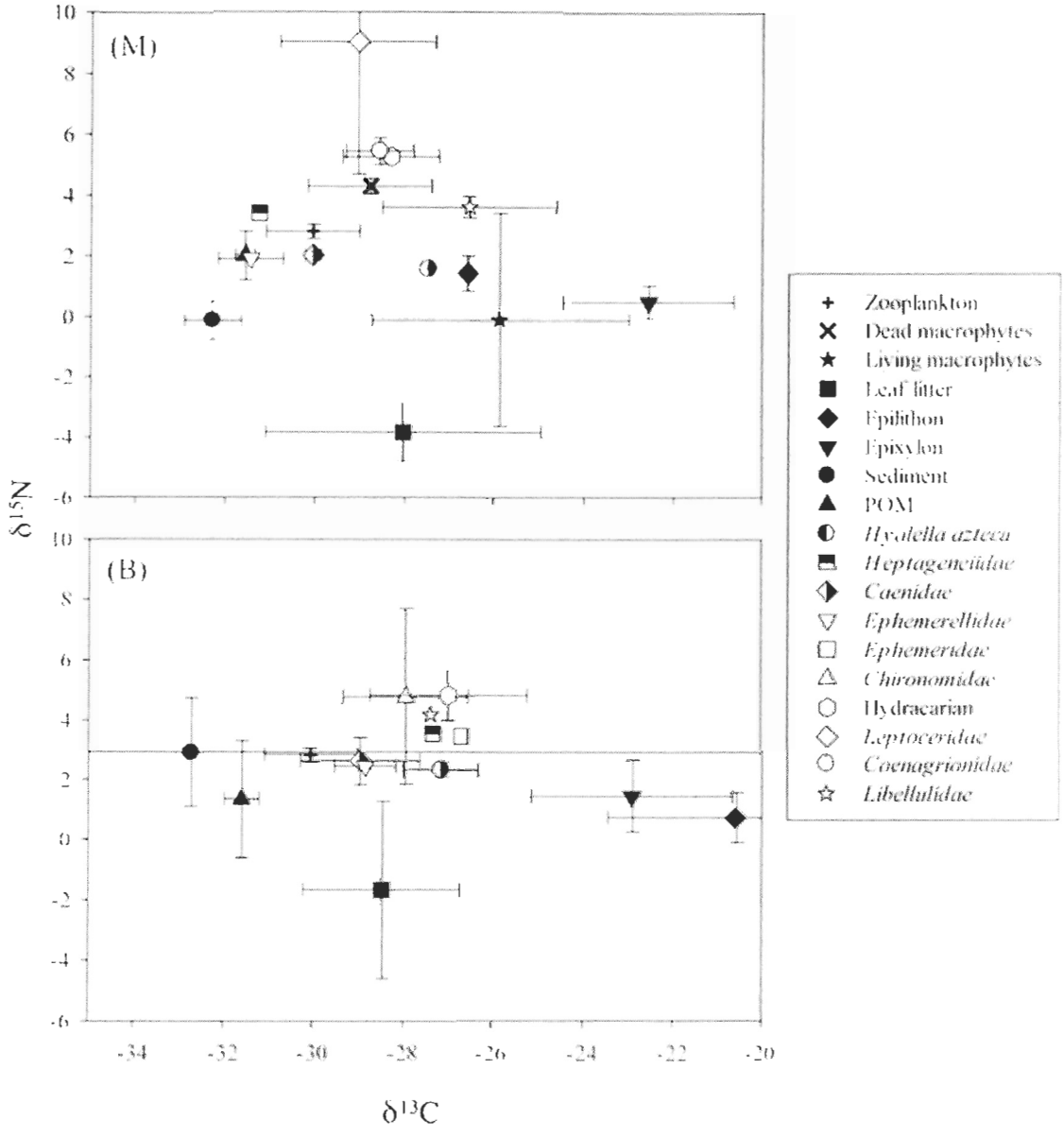

Figure 6. $\delta^{13}C$ and $\delta^{15}N$ of potential food sources and consumers for the lake De l'Est at sites with (M) and without (B) macrophytes. Error bars represent the mean ± SD.

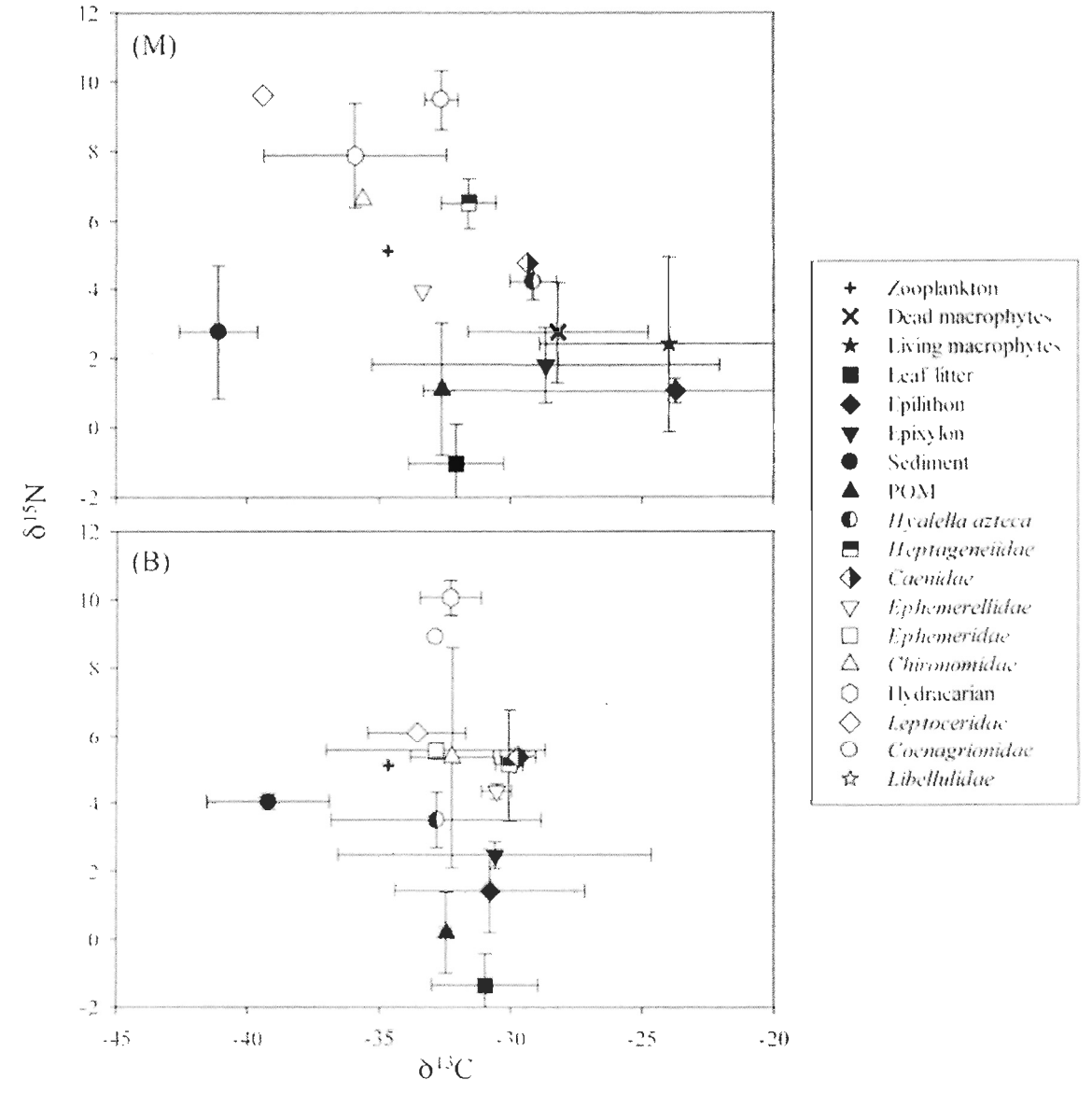

Figure 7. $\delta^{13}C$ and $\delta^{15}N$ of potential food sources and consumers for the lake Macpès at sites with (M) and without (B) macrophytes. Error bars represent the mean ± SD.

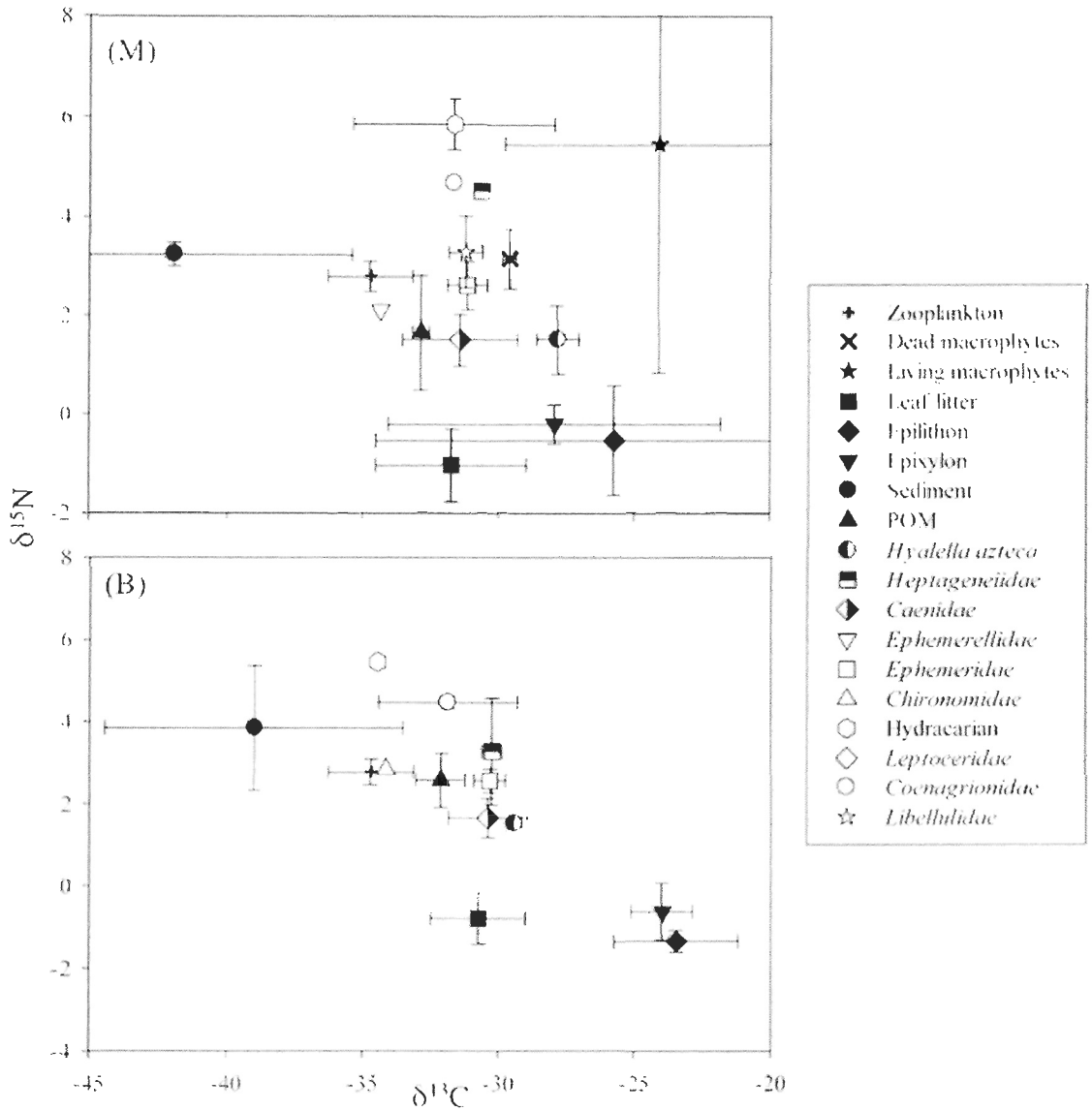

Figure 8. $\delta^{13}C$ and $\delta^{15}N$ of potential food sources and consumers for the lake Petit Touradi at sites with (M) and without (B) macrophytes. Error bars represent the mean ± SD.

Annexe 1. $\delta^{13}C$, $\delta^{15}N$ and C/N of potential food sources and consumers at sites with macrophytes for the seven lakes

Lakes	Samples	Mean (SD) δ13C	Mean (SD) δ15N	Mean (SD) C/N
Noir	Zooplankton	-35.63 (0.90)	4.66 (0.25)	6.31 (0.26)
	Macrophyte living	-24.04 (2.27)	1.36 (1.77)	15.11 (2.07)
	Macrophyte dead	-22.15 (0.21)	-6.58 (0.13)	17.16 (0.13)
	DOM	-8.75 (3.95)	0.10 (1.84)	68.24 (9.71)
	Epilithon	-16.85 (0)	0.28 (0)	10.90 (0)
	Epixylon	-23.00 (0)	2.25 (0)	24.70 (0)
	Leaf litter	-29.98 (0.64)	0.47 (0.81)	31.53 (6.78)
	POM	-31.02 (0.004)	2.49 (0.42)	12.69 (0.63)
	Amphipod	-30.51 (0.41)	2.58 (0.73)	6.10 (0.73)
	Caenidae	-32.43 (1.49)	2.53 (0.75)	6.46 (0.30)
	Hydracarian	-32.60 (1.66)	5.71 (1.08)	5.92 (0.07)
	Ephemerellidae	-34.14 (1.85)	2.80 (0.27)	7.02 (1.2)
	Chironomidae	-29.39 (0)	3.97 (0)	6.10 (0)
	Coenagrionidae	-31.91 (0.96)	5.85 (0.26)	5.52 (0.16)
Neigette	Zooplankton	-37.29 (0.80)	7.80 (0.36)	6.03 (0.13)
	Macrophyte living	-24.49 (3.81)	4.79 (2.78)	12.56 (1.16)
	Macrophyte dead	-29.01 (0)	3.18 (0)	28.70 (0)
	DOM	-4.50 (1.08)	2.82 (0.75)	45.61 (1.44)
	Epilithon	-11.10 (0)	3.40 (0)	21.20 (0)
	Epixylon	-23.16 (1.59)	4.59 (0.16)	17.94 (1.49)
	Leaf litter	-30.75 (2.43)	2.04 (1.77)	30.53 (8.63)
	POM	-31.02 (0)	2.19 (0)	11.50 (0)
	Sediment	-50.20 (0)	2.04 (0)	9.20 (0)
	Amphipod	-32.72 (0)	5.99 (0)	6.10 (0)
	Caenidae	-35.50 (0.72)	6.21 (0.61)	5.97 (0.33)
	Hydracarian	-32.18 (0.56)	10.46 (0.72)	5.03 (0.57)
	Leptoceridae	-35.64 (0)	12.83 (0)	6.70 (0)
	Ephemerellidae	-33.48 (0)	6.16 (0)	6.97 (0)
	Chironomidae	-36.64 (0.86)	7.18 (0.39)	5.96 (0.34)
	Coenagrionidae	-33.28 (0.79)	9.25 (0.96)	5.47 (0.13)
	Libellulidae	-32.59 (1.42)	7.63 (0.89)	5.14 (0.24)

Lakes	Samples	Mean (SD) δ13C	Mean (SD) δ15N	Mean (SD) C/N
Des Baies	Zooplankton	-34.21 (0.13)	0.89 (0.65)	6.53 (1.18)
	Macrophyte living	-22.14 (5.04)	-1.43 (6.17)	16.89 (8.03)
	Macrophyte dead	-23.64 (5.31)	4.16 (3.14)	17.83 (10.02)
	DOM	-8.76 (2.65)	0.06 (1.77)	44.24 (14.31)
	Epilithon	-24.52 (3.13)	0.47 (1.71)	17.84 (1.48)
	Epixylon	-26.69 (1.23)	-0.04 (2.08)	30.56 (12.04)
	Leaf litter	-27.88 (0.76)	-1.16 (0.54)	19.76 (11.63)
	POM	-29.12 (1.40)	4.11 (0.20)	12.14 (2.03)
	Sediment	-36.42 (6.29)	2.37 (1.41)	10.44 (1.09)
	Amphipod	-26.89 (1.31)	0.64 (0.15)	6.82 (0.36)
	Caenidae	-31.46 (0)	0.98 (0)	5.33(0)
	Heptageneiidae	-29.89 (0)	1.56 (0)	6.50 (0)
	Hydracarian	-29.21 (0)	5.11 (0)	5.63 (0)
	Leptoceridae	-21.00 (1.02)	3.04 (0.02)	6.14 (0.64)
	Ephemeridae	-26.91 (1.17)	0.97 (1.03)	5.46 (0.27)
	Ephemerellidae	-29.11 (1.95)	0.45 (1.76)	6.68 (0.05)
	Coenagrionidae	-28.36 (1.25)	4.82 (0.16)	5.79 (0.47)
	Libellulidae	-27.20 (2.21)	2.38 (0.56)	5.71 (0.05)
Ferré	Zooplankton	-34.34 (4.73)	3.67 (0.58)	6.28 (0.30)
	Macrophyte living	-26.78 (3.50)	3.66 (1.11)	16.98 (1.71)
	Macrophyte dead	-29.14 (2.02)	3.02 (0.58)	48.07 (15.72)
	DOM	-5.68 (0.34)	0.19 (1.25)	57.48 (13.16)
	Epilithon	-20.44 (1.67)	3.61 (0.47)	13.79 (0.20)
	Epixylon	-25.81 (0)	2.30 (0)	19.90 (0)
	Leaf litter	-29.67 (1.28)	-1.29 (1.18)	29.33 (10.06)
	POM	-32.84 (0.72)	0.94 (2.71)	10.83 (4.81)
	Sediment	-33.81 (8.40)	2.65 (0.08)	9.14 (2.51)
	Amphipod	-32.77 (5.16)	3.84 (3.46)	6.06 (0.19)
	Caenidae	-32.75 (0.26)	4.42 (0.18)	5.72 (0.044)
	Heptageneiidae	-31.71 (0)	4.45 (0)	5.80 (0)
	Hydracarian	-32.12 (0.84)	9.48 (0.69)	5.76 (0.31)
	Leptoceridae	-33.49 (0.52)	9.98 (2.06)	6.43 (0.52)
	Ephemeridae	-33.83 (0.51)	5.61 (0.32)	5.34 (0.72)
	Ephemerellidae	-34.02 (1.31)	3.91 (0.31)	6.63 (0.38)
	Chironomidae	-30.31 (0.61)	5.84 (0.69)	5.27 (0.05)
	Coenagrionidae	-33.58 (0.46)	7.49 (0.67)	5.25 (0.31)
	Libellulidae	-31.72 (0.90)	5.92 (1.45)	5.30 (0.15)

Lakes	Samples	Mean (SD) δ13C	Mean (SD) δ15N	Mean (SD) C/N
	Zooplankton	-30.05 (1.04)	2.83 (0.24)	6.06 (0.12)
	Macrophyte living	-25.88 (2.86)	-0.10 (3.54)	18.99 (5.47)
	Macrophyte dead	-28.79 (1.38)	4.32 (0.25)	59.47 (10.09)
	DOM	-6.07 (3.89)	0.83 (2.34)	54.49 (5.35)
	Epilithon	-26.59 (0.08)	1.45 (0.58)	18.85 (2.47)
	Epixylon	-22.56 (1.89)	0.50 (0.52)	25.76 (7.86)
	Leaf litter	-28.045 (3.06)	-3.83 (0.97)	32.63 (12.72)
	POM	-31.55 (0.22)	2.04 (0.80)	10.30 (1.81)
De l'Est	Sediment	-32.29 (0.63)	-0.11 (0.65)	9.43 (1.39)
	Amphipod	-27.47 (0)	1.58 (0)	6.30 (0)
	Caenidae	-30.05 (0.16)	2.05 (0.03)	5.60 (0.04)
	Heptageneiidae	-31.25 (0)	3.43 (0)	6.80 (0)
	Hydracarian	-28.33 (1.07)	5.28 (0.17)	5.66 (0.41)
	Leptoceridae	-29.06 (1.73)	9.05 (4.33)	5.63 (0.31)
	Ephemerellidae	-31.43 (0.72)	1.93 (0.06)	6.69 (0.96)
	Coenagrionidae	-28.58 (0.75)	5.46 (0.44)	5.26 (0.15)
	Libellulidae	-26.5 (1.95)	3.64 (0.35)	5.24 (0.52)
	Zooplankton	-34.69 (0)	5.13 (0)	6.00 (0)
	Macrophyte living	-23.99 (4.91)	2.42 (2.54)	20.79 (8.38)
	Macrophyte dead	-28.20 (3.43)	2.76 (1.45)	54.52 (38.34)
	DOM	-17.58 (4.36)	3.11 (1.39)	55.29 (7.70)
	Epilithon	-23.75 (9.58)	1.08 (0.35)	16.45 (2.87)
	Epixylon	-28.67 (6.61)	1.82 (1.08)	18.71 (4.42)
	Leaf litter	-32.08 (1.82)	-1.03 (1.17)	39.75 (14.03)
	POM	-32.63 (0.15)	1.11 (1.90)	9.61 (2.21)
Macpès	Sediment	-41.08 (1.48)	2.75 (1.92)	11.61 (0.91)
	Amphipod	-29.14 (0.89)	4.23 (0.53)	6.35 (0.57)
	Caenidae	-29.37 (0)	4.77 (0)	5.47 (0)
	Heptageneiidae	-31.61 (1.04)	6.51 (0.70)	6.57 (0)
	Hydracarian	-35.91 (3.46)	7.87 (1.49)	6.67 (0.84)
	Leptoceridae	-39.40 (0)	9.60 (0)	5.20 (0)
	Ephemerellidae	-33.37 (0)	3.95 (0)	6.00 (0)
	Chironomidae	-35.62 (0)	6.62 (0)	7.20 (0)
	Coenagrionidae	-32.64 (0.63)	9.46 (0.84)	5.09 (0.24)

Lakes	Samples	Mean (SD) δ13C	Mean (SD) δ15N	Mean (SD) C/N
	Zooplankton	-34.74 (1.56)	2.78 (0.32)	5.77 (0.15)
	Macrophyte living	-24.10 (2.66)	4.79 (4.64)	21.58 (5.39)
	Macrophyte dead	-29.61 (0.25)	3.13 (0.61)	37.49 (11.75)
	DOM	-20.52 (0.64)	0.81 (1.03)	59.18 (5.71)
	Epilithon	-25.75 (8.76)	-0.53 (1.10)	15.29 (1.84)
	Epixylon	-27.94 (6.12)	-0.21 (0.39)	22.47 (8.02)
	Leaf litter	-31.74 (2.78)	-1.07 (0.76)	25.25 (8.24)
	POM	-32.88 (0.31)	1.64 (01.16)	13.42 (0.24)
Petit Touradi	Sediment	-41.94 (6.56)	3.23 (0.24)	12.22 (2.42)
	Amphipod	-27.81 (0.77)	1.49 (0.70)	6.75 (0.87)
	Caenidae	-31.43 (2.12)	1.49 (0.53)	6.24 (0.39)
	Heptageneiidae	-30.65 (0)	4.51 (0)	6.30 (0)
	Hydracarian	-31.65 (3.71)	5.85 (0.50)	5.73 (0.13)
	Ephemeridae	-31.16 (0)	2.60 (0.49)	5.42 (0.60)
	Ephemerellidae	-34.36 (0)	2.10 (0)	6.00 (0)
	Coenagrionidae	-31.66 (0)	4.68 (0)	5.25 (0)
	Libellulidae	-31.22 (0.62)	3.28 (0.74)	5.08 (0.46)

Annexe 2. $\delta^{13}C$, $\delta^{15}N$ an C/N of potential food sources and consumers at sites without macrophytes for the seven lakes

Lakes	Samples	Mean (SD) δ13C	Mean (SD) δ15N	Mean (SD) C/N
Noir	Zooplankton	-35.62 (0.90)	4.66 (0.25)	6.31 (0.26)
	DOM	-6.84 (0)	-0.42 (0)	53.10 (0)
	Epilithon	-27.31 (2.26)	2.83 (1.98)	17.38 (1.11)
	Epixylon	-24.39 (1.74)	0.64 (0.46)	20.27 (5.42)
	Leaf litter	-30.15 (1.15)	-0.51 (1.24)	31.11 (2.89)
	POM	-31.76 (0.47)	1.65 (3.25)	10.16 (2.33)
	Sediment	-34.58 (12.99)	3.70 (1.36)	12.99 (2.82)
	Amphipod	-26.23 (2.09)	2.79 (0.43)	6.42 (0.37)
	Caenidae	-31.19 (0.05)	3.49 (0.51)	5.87 (0.92)
	Heptageneiidae	-33.30 (0.91)	4.84 (1.39)	7.13 (0.53)
	Hydracarian	-33.66 (0.45)	9.00 (0.99)	6.95 (0.05)
	Leptoceridae	-25.81 (4.54)	4.31 (0.61)	6.21 (0.36)
	Ephemerellidae	-33.34 (2.47)	3.51 (1.32)	7.78 (0.56)
	Chironomidae	-29.73 (0.09)	3.89 (0.37)	5.43 (0.09)
	Coenagrionidae	-31.77 (0.49)	7.47 (0.45)	5.16 (0.05)
	Libellulidae	-36.11 (0)	5.23 (0)	6.45 (0)
Neigette	Zooplankton	-37.29 (0.80)	7.80 (0.36)	6.03 (0.13)
	DOM	-8.31 (6.37)	2.00 (0.44)	44.74 (0.51)
	Epilithon	-13.91 (2.89)	3.69 (1.71)	26.55 (6.38)
	Epixylon	-23.01 (1.18)	4.32 (0.35)	15.47 (1.87)
	Leaf Litter	-29.79 (1.45)	-1.08 (1.30)	46.94 (23.60)
	POM	-33.61 (0.07)	5.40 (0.21)	10.87 (0.04)
	Sediment	-36.40 (7.85)	4.22 (1.14)	11.43 (3.01)
	Amphipod	-31.23 (0.73)	5.99 (0.33)	6.71 (0.48)
	Caenidae	-31.84 (0.47)	6.67 (0.15)	5.85 (0.46)
	Heptageneiidae	-32.79 (1.00)	5.90 (2.29)	6.96 (0.78)
	Hydracarian	-31.97 (0.82)	10.16 (0.91)	4.97 (0.05)
	Leptoceridae	-33.48 (0)	11.38 (0)	5.50 (0)
	Ephemerellidae	-34.17 (1.08)	5.63 (0.07)	7.30 (0.51)
	Chironomidae	-32.60 (1.40)	6.91 (0.42)	6.43 (0.79)
	Coenagrionidade	-33.10 (0.48)	9.21 (0.42)	5.45 (0.28)
	Libellulidae	-31.43 (2.46)	8.20 (0.19)	5.27 (0.32)

Lakes	Samples	Mean (SD) δ13C	Mean (SD) δ15N	Mean (SD) C/N
	Zooplankton	-34.21 (0.13)	0.89 (0.65)	6.53 (1.18)
	DOM	-10.56 (3.87)	1.97 (3.23)	50.73 (2.91)
	Epilithon	-24.35 (5.63)	0.33 (1.81)	17.93 (1.41)
	Epixylon	-24.24 (4.29)	-0.51 (0.73)	26.05 (6.87)
	Leaf Litter	-30.00 (4.03)	-1.74 (0.57)	36.27 (14.90)
	POM	-29.09 (1.22)	3.45 (1.69)	12.75 (0.95)
	Sediment	-37.69 (17.60)	2.32 (1.66)	10.433 (5.15)
	Amphipod	-25.59 (2.31)	0.81 (0.50)	6.77 (0.73)
Des Baies	Caenidae	-29.95 (0.96)	0.55 (0.43)	5.71 (0.45)
	Heptageneiidae	-28.93 (1.39)	1.88 (4.01)	6.66 (1.47)
	Hydracarian	-33.57 (0)	3.29 (0)	5.98 (0)
	Leptoceridae	-27.87 (0)	3.72 (0)	6.24 (0.59)
	Ephemeridae	-29.05 (0)	1.09 (0)	5.64 (0)
	Ephemerellidae	-29.34 (2.41)	-1.35 (1.32)	6.75 (0.76)
	Chironomidae	-25.53 (3.32)	3.65 (0.61)	5.39 (0.80)
	Coenagrionidade	-26.96 (1.86)	4.16 (0.70)	5.80 (0.41)
	Libellulidae	-26.14 (0)	3.20 (0)	5.54 (0)
	Zooplankton	-34.34 (4.73)	3.67 (0.58)	6.28 (0.30)
	DOM	-6.59 (3.90)	2.32 (3.16)	57.01 (1.72)
	Epilithon	-23.63 (2.23)	2.48 (0.48)	16.11 (4.00)
	Epixylon	-26.60 (0.74)	3.26 (0.83)	12.74 (1.09)
	Leaf Litter	-30.42 (1.60)	-2.29 (1.27)	25.74 (9.10)
	POM	-32.14 (0.09)	2.96 (1.26)	14.36 (0.59)
	Sediment	-37.99 (2.20)	2.27 (0.93)	8.41 (1.19)
Ferré	Amphipod	-27.56 (1.87)	3.55 (0.65)	5.55 (0.98)
	Heptageneiidae	-30.95 (1.25)	4.15 (2.03)	6.46 (0.16)
	Hydracarian	-32.27 (1.54)	9.53 (0.53)	6.04 (0.45)
	Leptoceridae	-30.41 (1.62)	7.12 (2.47)	6.03 (0.28)
	Ephemeridae	-30.71 (1.45)	6.11 (0.21)	5.52 (0.20)
	Ephemerellidae	-29.91 (0.48)	3.21 (0.71)	6.76 (0.26)
	Chironomidae	-29.27 (0.62)	5.70 (0.80)	6.16 (0.45)
	Coenagrionidade	-32.08 (0)	7.59 (0)	5.37 (0)
	Zooplankton	-30.05 (1.04)	2.83 (0.24)	6.06 (0.12)
	DOM	-4.41 (1.49)	0.70 (0.24)	52.04 (3.27)
	Epilithon	-20.57 (2.88)	0.75 (0.84)	16.41 (2.78)
	Epixylon	-22.90 (2.24)	1.46 (1.20)	22.94 (6.77)
	Leaf Litter	-28.47 (1.76)	-1.67 (1.95)	29.86 (3.40)
	POM	-31.59 (0.39)	1.36 (1.97)	10.45 (2.60)
	Sediment	-32.71 (13.92)	2.91 (1.81)	11.88 (4.12)
De l'Est	Amphipod	-27.14 (0.84)	2.33 (0.26)	6.68 (0.38)
	Caenidae	-28.97 (1.32)	2.62 (0.80)	5.45 (0.27)
	Heptageneiidae	-27.34 (0)	3.55 (0)	5.90 (0)
	Hydracarian	-27.01 (1.75)	4.82 (0.83)	5.71 (0.51)
	Ephemeridae	-26.71 (0)	3.47 (0)	5.66 (0)
	Ephemerellidae	-28.85 (0.68)	2.44 (0.08)	6.30 (0.59)
	Chironomidae	-27.95 (1.39)	4.76 (2.92)	5.69 (0.78)
	Libellulidae	-27.40 (0)	4.19 (0)	5.20 (0)

Lakes	Samples	Mean (SD) δ13C	Mean (SD) δ15N	Mean (SD) C/N
Macpès	Zooplankton	-34.69 (0)	5.13 (0)	6.00 (0)
	DOM	-7.94 (0.82)	1.23 (1.02)	53.65 (1.85)
	Epilithon	-30.80 (3.62)	1.43 (1.23)	15.63 (0.37)
	Epixylon	-30.61 (5.96)	2.49 (0.38)	16.13 (2.58)
	Leaf Litter	-30.98 (2.03)	-1.35 (0.92)	30.92 (9.76)
	POM	-32.48 (0.20)	0.20 (1.20)	7.89 (1.41)
	Sediment	-39.21 (2.32)	4.05 (0.23)	11.50 (1.69)
	Amphipod	-32.83 (4.00)	3.51 (0.81)	6.56 (1.56)
	Caenidae	-29.73 (0.68)	5.38 (0.23)	5.69 (0.18)
	Heptageneiidae	-30.07 (0.52)	5.14 (1.65)	6.83 (1.39)
	Hydracarian	-32.33 (1.16)	10.04 (0.51)	5.86 (0.25)
	Leptoceridae	-33.59 (1.85)	6.11 (0.09)	5.90 (0.06)
	Ephemeridae	-32.85 (4.16)	5.56 (0.24)	5.34 (0.36)
	Ephemerellidae	-30.54 (0.57)	4.34 (0.22)	6.28 (0.17)
	Chironomidae	-32.25 (1.59)	5.35 (3.24)	5.59 (0.11)
	Coenagrionidade	-32.88 (0)	8.90 (0)	5.16 (0)
Petit Touradi	Zooplankton	-34.74 (1.56)	2.78 (0.32)	5.77 (0.15)
	DOM	-15.98 (0.86)	3.11 (0.55)	66.70 (4.25)
	Epilithon	-23.48 (2.28)	-1.34 (0.27)	12.10 (0.68)
	Epixylon	-23.99 (1.11)	-0.62 (0.71)	30.14 (13.28)
	Leaf Litter	-30.75 (1.74)	-0.78 (0.62)	39.86 (2.11)
	POM	-32.16 (0.92)	2.58 (0.65)	13.68 (2.97)
	Sediment	-39.03 (5.44)	3.85 (1.52)	7.69 (1.51)
	Amphipod	-29.44 (0.26)	1.53 (0.06)	6.67 (0.77)
	Caenidae	-30.41 (1.44)	1.67 (0.47)	6.14 (0.46)
	Heptageneiidae	-30.28 (0.36)	3.28 (1.30)	7.59 (1.27)
	Hydracarian	-34.52 (0)	5.45 (0)	5.71 (0)
	Ephemeridae	-30.34 (0.57)	2.57 (0.29)	5.64 (0.78)
	Chironomidae	-34.20 (0)	2.85 (0)	6.40 (0)
	Coenagrionidade	-31.91 (2.56)	4.47 (0.15)	5.48 (0.37)

CHAPITRE 2
CONCLUSION

Cette étude a permis, par traçage isotopique et à l'aide de modèles de mélange, de caractériser le régime alimentaire des principaux macro-invertébrés occupant les habitats littoraux colonisés ou non par des macrophytes dans sept lacs boréaux. Elle contribue aussi à améliorer notre compréhension des transferts énergétiques et de MO au sein des réseaux trophiques benthiques littoraux. Par ailleurs, cette étude permet d'intégrer les apports de carbone allochtone dans les paradigmes sur le fonctionnement des écosystèmes lacustres, pour mieux comprendre les transferts d'énergie à la base des réseaux trophiques.

Les analyses isotopiques témoignent de l'assimilation intégrée des sources de nourritures par les consommateurs sur une certaine période de temps, celle-ci correspondant au taux de renouvellement du tissu d'un organisme (Kling *et al.* 1992). Le modèle linéaire mixte de mélange utilisé pour analyser les résultats isotopiques possède ses forces et ses faiblesses. Tout d'abord, ce modèle permet de ne pas sous-estimer les principales sources de nourritures et de ne pas surestimer les sources de nourriture qui sont moins utilisées pas les consommateurs. En second lieu, ce modèle prend en compte le fractionnement différent du carbone et de l'azote qui varie en fonction du type de tissus, végétal ou animal, ingéré par les organismes. Par contre, il est possible d'avoir d'autres sources de nourritures que celles intégrées au modèle ou encore, d'avoir un mauvais facteur de fractionnement pour un type de tissus donné. Malgré tout, ce modèle permet d'estimer la contribution relative des sources de nourritures à la diète des consommateurs de façon assez fiable, pour un site et une période de temps donnée, soit le taux de renouvellement du tissu d'un organisme.

Les réseaux trophiques benthiques des lacs étudiés comportent trois niveaux. Tout d'abord, les invertébrés benthiques herbivores/détritivores composés des amphipodes *H. azteca* et des éphéméroptères *Caenidae*, *Heptageneiidae* et *Ephemerellidae*. Les éphéméroptères *Ephemeridae*, les diptères *Chironomidae,* les libellules *Anisoptera Libellulidae* et les demoiselles *Zygoptera Coenagrionidae* se trouvent au second niveau trophique ce sont soit des omnivores ou des carnivores tout comme les trichoptères *Leptoceridae* qui se trouvent au troisième niveau trophique. Afin d'avoir un schéma complet du réseau trophique benthique, il serait intéressant que des études futures échantillonnent aussi les poissons benthiques.

Les invertébrés benthiques herbivores/détritivores (les amphipodes *H. azteca* et les éphéméroptères *Caenidae* sp., *Heptageneiidae* sp, et *Ephemerellidae* sp.) des lacs que nous avons étudiés se nourrissent principalement sur des détritus de feuilles de plantes terrestres, donc du carbone allochtone. Par contre, la contribution relative des détritus de feuilles de plantes terrestres à la diète de ces invertébrés est un peu moins grande aux sites ayant des macrophytes qu'aux sites n'en ayant pas. Malgré tout, les apports terrigènes semblent être importants pour tous les réseaux trophiques benthiques littoraux des lacs échantillonnés tant pour les milieux contenant des macrophytes que ceux n'en ayant pas.

Bien que les détritus de feuilles de plantes terrestres soient la principale source de carbone utilisée, lorsque le milieu ne contient pas de macrophytes, la consommation de périphyton est une source non négligeable pour les consommateurs primaires du milieu littoral benthique. Par contre lorsque les macrophytes sont présents, la contribution relative du périphyton est moins importante que la contribution relative des macrophytes à la diète des consommateurs primaires. De plus, les invertébrés semblent assimiler les macrophytes principalement quand ils se retrouvent sous forme détritique. Lorsque les macrophytes étaient présents, l'épiphyton pouvait être une source de nourriture potentielle pour les

invertébrés étudiés. En effet, plusieurs auteurs considèrent que cette forme algale constitue une composante importante du régime alimentaire de plusieurs herbivores (Bunn et Boon 1993; James *et al.* 2000a; Herwig *et al.* 2004). Des études futures devraient donc envisager de prendre en considération l'épiphyton dans les analyses des régimes alimentaires des invertébrés benthiques littoraux.

Pour ce qui est des organismes omnivores (les éphéméroptères *Ephemeridae* sp. et les diptères *Chironomidae* sp.) et des carnivores (les trichoptères *Leptoceridae* sp., et les libellules *Anisoptera Libellulidae* sp. et les demoiselles *Zygoptera Coenagrionidae* sp.) les régimes alimentaires sont très variés en fonction des familles et en fonction des lacs. Aussi, les résultats décrivant la diète de ces espèces sont parfois contradictoires. Ces résultats peuvent s'expliquer par la multiplicité des sources de nourritures possible. En effet, il est possible que toutes les sources de nourritures et les proies des omnivores et des carnivores n'aient pas été échantillonnées ce qui pourrait expliquer les résultats obtenus.

L'identification des macro-invertébrés a été faite jusqu'à la famille. Plusieurs familles de macrobenthos peuvent avoir des espèces ayant différents régimes alimentaires (Merritt et Cummins 1996). Dans cette étude, l'identification s'est faite jusqu'à la famille, il est donc possible que nous ayons regroupé des espèces avec des régimes alimentaires différents. Des études futures devraient envisager de pousser l'identification des macro-invertébrés jusqu'à l'espèce afin d'avoir une précision accrue des résultats, tant au niveau des organismes herbivores, détritivores, qu'omnivores et prédateurs.

Perspectives

Cette étude porte sur des lacs oligotrophes du Bas-St-Laurent. Dans une optique où plusieurs lacs ont un processus d'eutrophisation accéléré, entre autres, par la pollution, il

serait intéressant de réaliser une étude comparable avec des lacs de différents niveaux trophiques afin de vérifier si les principaux résultats seraient semblables pour des lacs mésotrophes et eutrophes. Comparer les réseaux trophiques de lacs ayant différents niveaux trophiques permettrait d'apporter des connaissances sur l'évolution des réseaux trophiques lorsqu'un lac évolue vers un milieu eutrophe. Aussi comme l'importance des macrophytes dans les réseaux trophiques est variable selon les lacs, les espèces présentes et les saisons (Lodge 1991 ; Jacobsen et Sand-Jensen 1992, 1995), une plus grande diversité de niveaux trophiques aiderait à la compréhension de l'intégration des macrophytes dans les différents réseaux trophiques.

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